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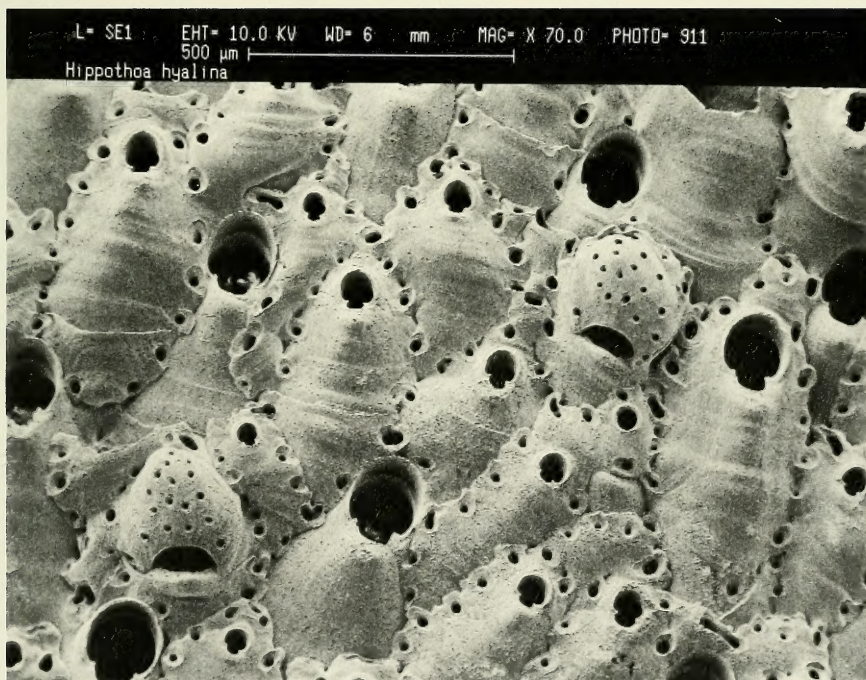
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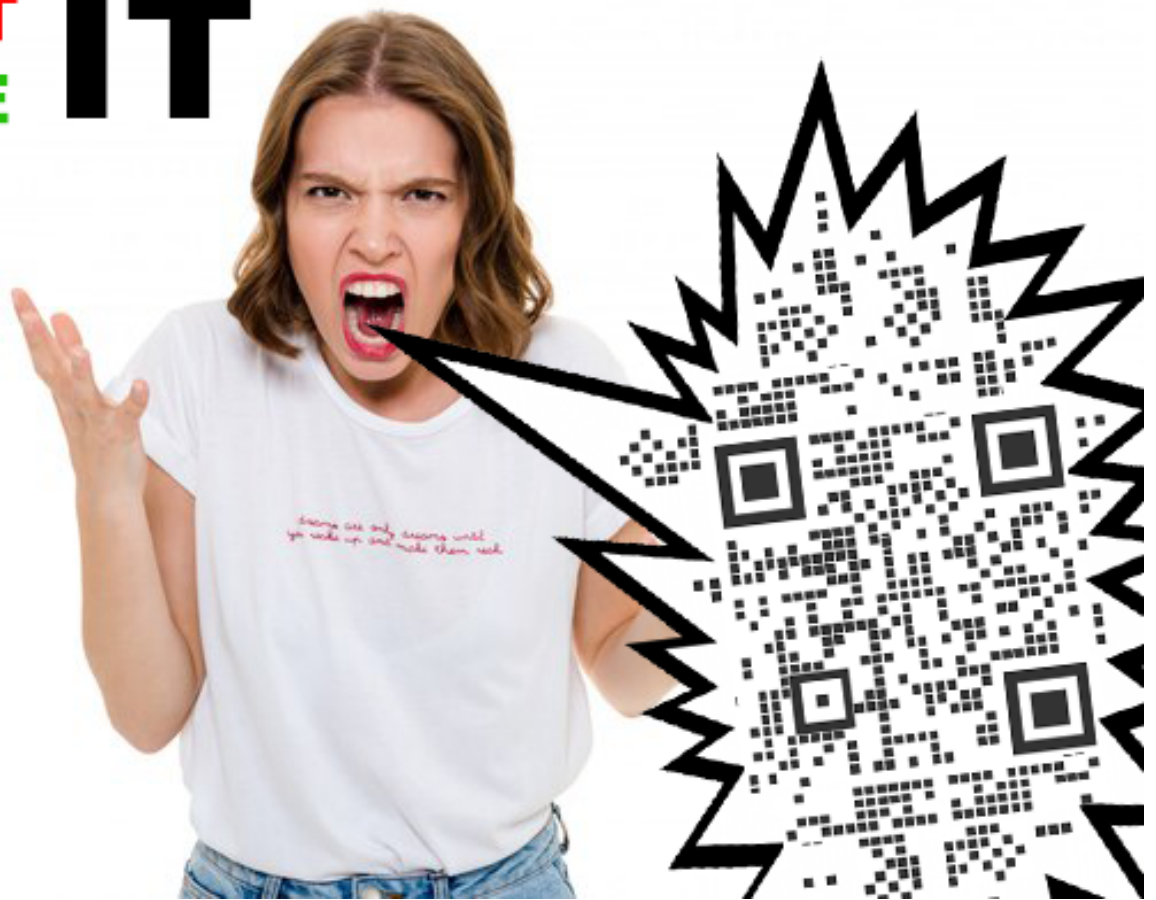
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Bryozoans, Hermit Crabs, and Gastropods: Life Strategies Can Affect the Fossil Record

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Abstract. — Epizootic associations among bryozoans, hermit crabs, and gastropod shells are not chance occurrences, but constitute a relationship that may benefit the bryozoan, and possibly the hermit crab. Gastropod shells from Recent Texas gulf coast localities and fossil and Recent Pacific coast localities were examined. Texas gastropod shells occupied by hermit crabs and their bryozoan epifauna were compared with unoccupied shells. In summer all available shells were occupied by hermit crabs, and all occupied shells found were encrusted by bryozoans.

In winter in Texas no bryozoans encrusted intact *Polinices* shells unoccupied by hermit crabs; 33% of *Thais* shell fragments contained bryozoans and all *Busycon* spp. shells or fragments contained bryozoans.

Distinctive differences were found in encrusting patterns of hermit crab occupied and unoccupied shells. Similar bryozoan encrusting patterns were found on shells occupied by hermit crabs from California and Texas. These data can be used for interpreting the incidence of hermit crab occupation in both fossil and Recent gastropod shells.

Epizootic associations among bryozoans, hermit crabs, and gastropods or gastropod shells, represent a relationship that has existed since Jurassic times (Glaessner 1969; Palmer and Hancock 1973; Taylor 1976). Such fossil associations have also been described in more recent periods; e.g., by Roger and Buge (1947), Walter (1969), Buge and Fischer (1970), Taylor and Cook, (1981) and Walker (1988). Modern occurrences have been noted, for example, by Kirkpatrick and Metzelaar (1922), Cook (1968), Gordon (1972), Taylor and Cook (1981), Baluk and Radwanski (1984), and Bishop (1987). In west Africa, Cook (1968, p. 127) found that one species of encrusting bryozoan, *Membranipora commensale*, was primarily found on gastropod shells occupied by hermit crabs.

The preference of bryozoans for specific substrates has been well documented (Pinter 1969; Rogick and Croasdale 1949; Ryland 1976; Winston and Eiseman 1980). In selecting substrates, larvae may explore and inspect sites before attachment and metamorphosis (Woollacott and Zimmer 1971; Crisp 1974), and some species exhibit preferential settling to the extent of selecting concave surfaces as opposed to convex surfaces (Ryland 1959; Ryland and Gordon 1976; Bishop 1988). Walker (1988) found that bionts would not settle on tethered *Olivella* shells that were not occupied by hermit crabs.

The purpose of the following study was to document whether bryozoans encrusting gastropod shells occupied by hermit crabs more frequently select one part

of the shell over another, and to provide further documentation on whether hermit crab occupation can be determined in fossil gastropod assemblages. Interpretation may then be made as to whether gastropod shells are in their original habitat, or have been moved to other locations by hermit crabs (Frey 1987).

Materials and Methods

Modern gastropod shells inhabited by hermit crabs were collected in the spring from California and summer from Texas coasts. Gastropod shells, unoccupied by hermit crabs in winter, were collected from Texas. The assemblages of shells were analyzed for the following:

- (1) Identification of gastropod shells, epizootic bryozoans, and presence or absence of associated hermit crabs.
- (2) Encrusting sites of bryozoans.
- (3) The presence of other epizootic species on shells occupied by hermit crabs.

The broken shells that were collected in December 1988 from Texas were restricted to shells and fragments similar to those occupied by hermit crabs in the summer months.

Pliocene and Pleistocene fossils from the Pacific coast of North American were examined in collections of the University of California, Museum of Paleontology, Berkeley (UCP).

Results

Fifteen trochid gastropod shells (*Tegula funebris*) occupied by hermit crabs were collected in the spring from Rockaway Beach, California (Fig. 1). The hermit crab was *Pagurus samuelis*, a species which prefers rocky shores lacking sand, mainly in upper and middle intertidal zones, from Vancouver to Baja California (Reese 1969; Haig and Abbott 1980). The encrusting bryozoan was *Hippothoa hyalina* (Table 1).

Sixty gastropod shells inhabited by the hermit crab *Isocheles wurdmanni*, a filter feeder living along exposed coasts (Fotheringham 1976), were collected in the summer from the Texas coast (Figs. 2A, 2B). Of these, 15 were from the gulf side of the Bolivar Peninsula, 20 were from the entrance to the Galveston Ship Channel, and 25 were from the gulf side of San Luis Pass. The number and identity of each gastropod species is listed in Table 2.

Fifty one gastropod shells were collected in the winter months from the gulf side of Galveston Island. All of the shells lacked hermit crab occupants and were trapped among the rocks composing the jetties. No hermit crab occupied shells were found. The number and identity of each gastropod species is listed in Table 3.

Hippothoa hyalina was found on all hermit crab occupied *Tegula* shells collected in California in April 1972. *Membranipora arborescens* was found on all hermit crab occupied shells collected in Texas in August 1985. In addition, the gastropod *Crepidula plana* was found attached to the gastropod *Polinices*. *Crepidula* is frequently found in association with hermit crabs (Abbott and Haderlie 1980).

In comparison, some of the broken and entire shells collected from Galveston Island in the winter months in 1988 lacked encrustations of either bryozoans or other epibionts. None of the *Polinices* shells were encrusted with, or had indications of the past presence, of bryozoans or any other encrusting organism. The

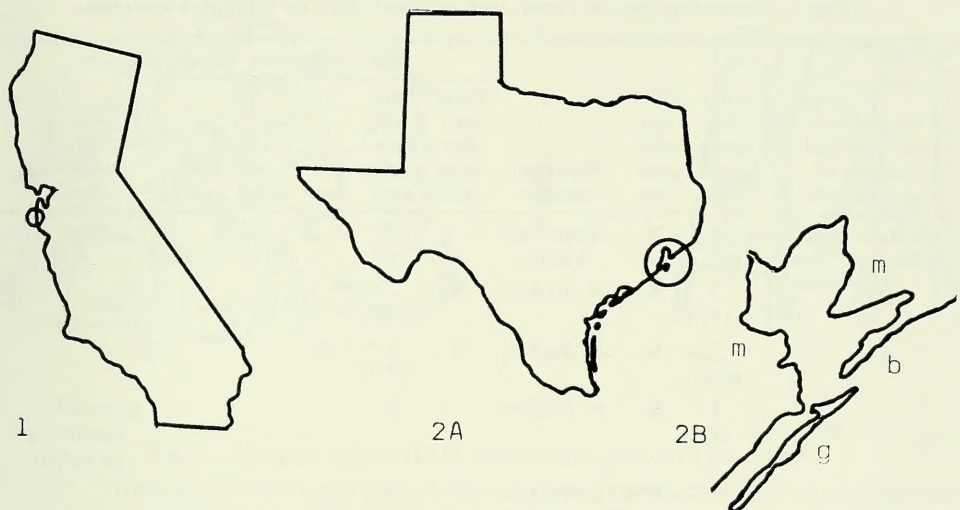


Fig. 1. Map of California. Region of Rockaway Beach is circled.

Fig. 2. Map of Texas. A. Region of Galveston and Bolivar Peninsula is circled. B. Galveston Island (g), and Bolivar Peninsula (b) are indicated in respect to the mainland (m).

other shells or shell fragments collected did not yield the same concise results (Table 3), but none contained burrowing bryozoans or the green alga *Enteromorpha*, nor were they entirely covered on the exterior by *Membranipora arborescens*.

Burrowing bryozoans were found on two species of gastropod shells inhabited by hermit crabs (Table 2). Others have found similar results: for example Gordon (1972, Goat Island, New Zealand); J. D. Soule (unpubl., southern California tidal pools); and Smyth (1988, Guam). Burrowers have also been found on the aperture of the living infaunal gastropod *Olivella biplicata* at Bodega Bay, California (Walker 1985, 1988). Therefore, burrowers apparently cannot offer conclusive evidence that gastropods were dead and occupied by hermit crabs.

All Recent material has been deposited at Allan Hancock Foundation, University of Southern California, Los Angeles.

Ecology

California.—Rockaway Beach (Fig. 1) is a rocky intertidal environment characterized by high energy waves. In the summer months the hermit crab *Pagurus samuelis*, carrying the *Tegula* shell, can be seen among populations of living *T. funebris* in the upper tidal pools which are isolated during low tide. Shell material that is not utilized by hermit crabs seasonally is either trapped in rock crevices, broken up in the surf, or carried into deeper water and buried. The availability of gastropod shells is the single most important factor limiting hermit crab population size (Kellogg 1976).

Texas.—The sampled localities are on the gulf side of the Bolivar Peninsula (an elongated extension of the coast forming a sand spit), and the gulf side of the west and east end of Galveston Island, an offshore barrier island (Figs. 2A, 2B). Prevailing longshore currents are east to west. The localities are high energy

Table 1. Encrusting sites on hermit crab occupied shells for California specimens.

Gastropoda species (total number of specimens)	Num- ber speci- mens (%)	Her- mit crab pres- ent	Bryozoan species	Encrusting sites					Other encrusting species
				Inner sur- face outer lip	Inner lip: colu- mella area	Apex	Cover- ing shell	Hum- mock	
<i>Tegula funebris</i> (12)	5 (42)	X	<i>Hippothoa hyalina</i>		X				
	2 (17)	X	<i>H. hyalina</i>	X					
	2 (17)	X	<i>H. hyalina</i>	X	X	X			
	1 (8)	X	<i>H. hyalina</i>		X				spirorbid encrusting on colony
	1 (8)	X	<i>H. hyalina</i>	X	X				
	1 (8)	X	<i>H. hyalina</i>	X	X	X			<i>Balanus</i> sp. on colony

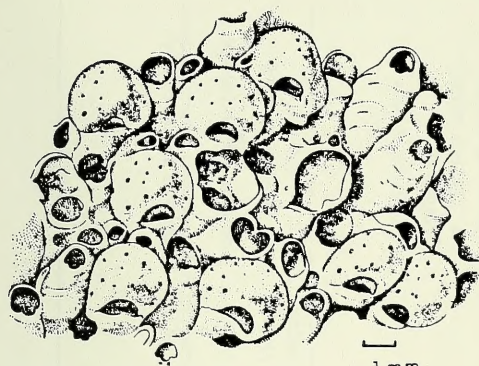
X = Present.

environments with sediments varying from well sorted sand and silty sand to shelly sand. Like the Rockaway Beach locality, shell material is rapidly broken up. The absence of empty shells, and the occupation of broken shells by hermit crabs in the summer months, is indicative of a limited supply (Back et al. 1976).

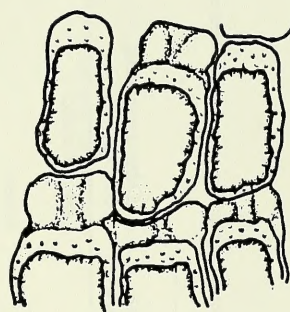
All of the shells occupied by hermit crabs were found in approximately the same ecological zone as the living snail. Of the shells collected, *Thais haemostoma* is found in shallow water on rocks and oyster reefs, *Polinices duplicatus* is found from low tide to 15 meters and both *Busycon spiratum* and *B. contrarium* are found intertidally.

Encrusting Bryozoans

The two species of bryozoans involved in the hermit crab association were *Hippothoa hyalina* (Pinter 1973; Morris 1980) on the Pacific coast, and *Membranipora arborescens* on the gulf coast (Lagaaij 1963, as *Conopeum commensale*: fide Cook 1968). *Hippothoa hyalina* (Fig. 3) is found in shallow waters distributed from Arctic to temperate waters in the northern hemisphere and in temperate waters in the southern hemisphere (Morris 1980). Geologically the species has been found as early as the Eocene. Along the Pacific Coast of North America the species can easily be separated from other multiseriel species belonging to this genus as it has a pleurilaminar growth form with both male and female zooids produced on secondary and subsequent layers, never the primary layer (Pinter 1973). *Membranipora arborescens* (Fig. 4), also found in shallow water, ranges from Morocco to the Gulf of Mexico. Cook (1968) stated that there had been a great deal of confusion separating the encrusting stage of *M. arborescens* from *M. commensale*. She also stated (1968, p. 123) that the encrusting stage of *Membranipora arborescens* has cryptocystal denticles, abundant chitinous spinules on



3



4

Fig. 3. *Hypothoa hyalina* (L). A multilaminar portion of the colony.

Fig. 4. *Membranipora arborescens* (Canu & Bassler). Opesia membrane is removed, showing thick cryptocyst with small spines, and fused block-like tubercles.

the frontal wall, and a brown line generally separating the zooids. The gulf coast colonies of *Membranipora arborescens* that were encrusted on hermit crab occupied shells in this study were pleurilaminar, never arborescent, had small cryptocystal denticles and chitinous spinules, and the brown line separating the zooids was irregularly present. The cryptocyst was thick, fused, and block-like tubercles were present. A few kenozooids were produced where growing edges meet, and sheets of zooids were large and regular. Occasionally the shell surface was etched.

Bryozoan Encrusting Patterns

Gulf Coast, Recent.—The initial sites of encrustation by the bryozoans are oriented in relation to the position of the crab in the shell. On the shells from the Gulf of Mexico (Fig. 5), the inner surface of the outer lip of the gastropod shell was above the anterior end of the crab and the inner lip (base of the columella) was below the anterior end (See Carleton and Roth 1975, for terminology). These two areas are usually colonized initially; subsequently colonies expand outward and over the gastropod shell surface (Fig. 6A, B). Analysis of colony edges indicates that fusion may take place, due either to recognition of sibling colonies or to fusing of single colony segments after growing apart (Chaney 1983). There were also scattered indications of redirected growth between nonsibling zooids (Chaney 1983). The data on the bryozoan encrusting sites are listed in Table 2.

California, Recent.—The hermit crab *Pagurus samuelis* occupies *Tegula funebris* shells. Initial points of bryozoan encrustation are above and/or below the anterior end of the crab, as indicated by the cheliped in Fig. 7B, C, after which colonies may expand and coalesce (Chaney 1983), eventually covering the exterior shell surface. Following the establishment of the bryozoan colonies, barnacles and spirorbid worms may settle on the bryozoans. As in the Texas specimens, there was either colony fusion of siblings or indications of redirected growth between nonsibling zooids (Chaney 1983). Data on the bryozoan encrusting sites are listed in Table 2.

Table 2. Encrusting sites on hermit crab occupied shells for Texas specimens.

Gastropoda species (total number of specimens)	Number specimens (%)	Hermit crab present	Bryozoan species	Encrusting sites				Other encrusting species
				Inner surface outer lip	Inner lip: columnella area	Apex	Covering shell	
<i>Polinices duplicatus</i> (23)	2 (9)	X	absent					<i>Enteromorpha</i>
	6 (26)	X	absent					Absent
	9 (39)	X	<i>Membranipora arborescens</i>	X			partial	
	3 (13)	X	Burrower <i>Terebripora</i> sp. <i>M. arborescens</i>					
	1 (4)	X	absent		X		partial	Burrowing sponge
	2 (9)	X	absent					<i>Balanus</i> sp.
	2 (6)	X	Burrower <i>Terebripora</i> sp. <i>M. arborescens</i> <i>M. arborescens</i>				partial	
	3 (10)	X		X		X		<i>Balanus</i> sp. on colony
	3 (10)	X	<i>M. arborescens</i>	X				<i>Balanus</i> sp. on colony
	14 (45)	X	<i>M. arborescens</i>	X	X		X	

Table 2. Continued.

Gastropoda species (total number of specimens)	Number specimens (%)	Hermit crab present	Bryozoan species	Encrusting sites					
				Inner surface outer lip	Inner lip: columella area	Apex	Covering shell	Hum- mock	Other encrusting species
<i>Thais haemostoma</i> (cont.)	3 (10)	X	<i>M. arborescens</i>	X	X				
	1 (3)	X	<i>M. arborescens</i> sm. unlaminar, dead		X				Burrowing sponge on colony
	1 (3)	X	<i>M. arborescens</i>	X	X		X		Sm. coral on colony
	4 (13)	X	<i>M. arborescens</i>	X	X	X			
<i>Busycon spiratum</i> (4)	3 (75)	X	<i>M. arborescens</i>	X	X	X			
	1 (25)	X	<i>M. arborescens</i>	X	X				
	1 (13)	X	<i>M. arborescens</i>	X	X				
<i>Busycon contrarium</i> (2)	1 (13)	X	<i>M. arborescens</i>	X	X				
	1	X	<i>M. arborescens</i>	X					<i>Balanus</i> sp. not on colony

X = Present.

Table 3. Encrusting sites of non-hermit crab occupied shells collected in winter months for Texas specimens.

Gastropoda species (total number of specimens)	Number specimens (%)	Bryozoan species	Encrusting sites				Other encrusting species
			Inner surface outer lip	Inner lip: columnella area	Apex	Covering shell	Hum- mock
<i>Polinices duplicatus</i> (8) All shells intact	8 (100)						
<i>Thais haemostoma</i> (18) All shells broken to some degree	3 (17)	<i>M. arborescens</i>	X	X			X
	3 (17)	etching <i>? M. arborescens</i>		X			
	6 (33)	<i>M. arborescens</i>	X				
<i>Busycon spiratum</i> (6) All broken to some degree	3 (75)	<i>M. arborescens</i>	X				
	3 (50)	etching	X				
<i>Busycon contrarium</i> (21) (61% broken)	3 (13)	<i>M. arborescens</i>	X				X
	2 (12)	<i>M. arborescens</i>	X	X	X		X
	11 (52)	<i>M. arborescens</i>	X				
	3 (13)	<i>M. arborescens</i>	X	X			X
	1 (15)	<i>M. arborescens</i>	X				
<i>Busycon contrarium</i>	1 (5)	<i>M. arborescens</i>	X	X			X
							Spirorbid
							Barnacles <i>Balanus</i> sp.

X = Present.

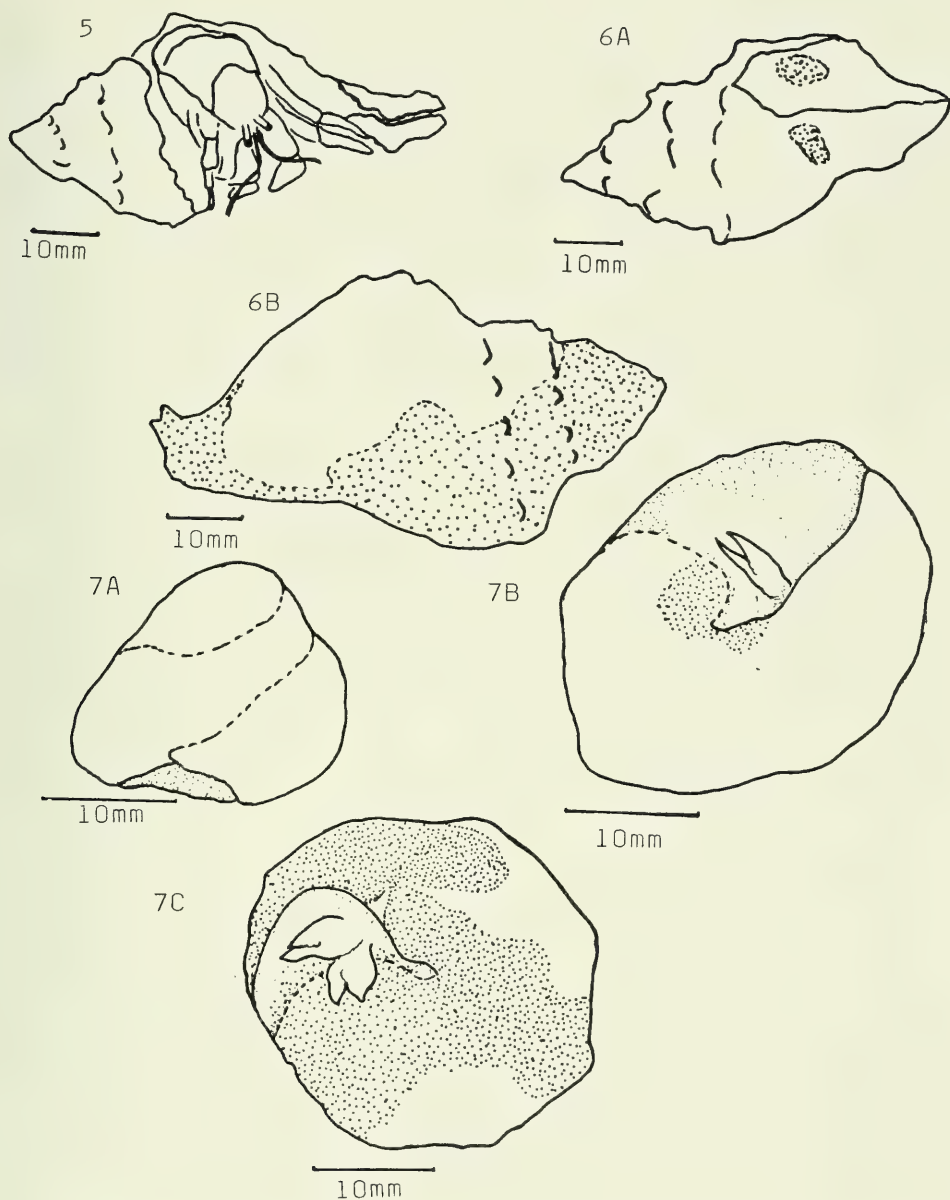


Fig. 5. *Thais haemostoma*, Galveston Island, Texas showing position of the crab in the shell.

Fig. 6. Encrusting Bryozoan sites on gastropods from Galveston Island area. 6A. Initial encrusting sites (coarse stippling) can be in either one or both places indicated. 6B. Subsequent colony expansion indicated (coarse stippling) on shell surface.

Fig. 7. Shell and encrusting sites on gastropod from Rockaway Beach. Side view of *Tegula funebris* with apertural region (light stippling) indicated. 7B. Bryozoan encrusting (coarse stippling) near aperture (light stippling). 7C. Bryozoan nearly covering apertural region (coarse stippling). Aperture is lightly stippled. Anterior end of hermit crab indicated by chelipeds.

Oregon, California, fossil.—Pliocene and Pleistocene bryozoan material from the Pacific Coast of North America was examined from the following localities: Elk River, Cape Blanco, Oregon (Pleistocene, Baldwin 1945); Moonstone Beach, near Arcata, California (Pliocene, Faustman 1964); Cape Blanco, (Pleistocene, Addicott 1964). All localities contained some shallow water elements and were, at least in part, characterized by an open coastline.

The Elk River sandstone (UCP-B7371) contained gastropod shells of *Fusitriton oregonensis* and *Nucella canaliculata*; both had evidence of probable hermit crab occupation. The bryozoan *Hippothoa hyalina* encrusted either on the apertural region and/or the inside upper lip. In several specimens bryozoan etchings were found on the interior upper lip as well as on the shell surface, indicating the existence of a hippothoid (Morris 1975). *Fusitriton oregonensis*, as well as other gastropods identified from this site but lacking bryozoans (*Epitonium indianorum*, *Olivella biplicata*), are found in Recent environments living on sandy bottom offshore, in shallow water, or on beaches. *Nucella canaliculata* prefers crawling on rocks (Abbott 1974). The presence of these gastropods in the fossil environment indicates that, before they were inhabited by hermit crabs and encrusted by *H. hyalina*, at least some shells were transported from other areas.

Moonstone Beach (UCP-B5525) specimens *Nucella canaliculata* and *N. lamellosa* are both shallow water gastropods which in modern environments are frequently found on rocks. In the area of Moonstone Beach that each was collected, no evidence of rocks was found. The deposit was composed of poorly lithified sandstone. The encrusting pattern of *Hippothoa hyalina* (inner upper lip, columella region) indicates the probable presence of hermit crabs occupying a sandy beach. Therefore it is reasonable to assume that there was some transportation of the shells after death of the living gastropod before occupation by hermit crabs occurred. Where parts of some colonies had been rubbed off, typical hippothoid etchings were visible.

A poorly consolidated conglomerate south of the lighthouse at Cape Blanco is primarily composed of the pelecypod *Tresus* (UCP-A8712). At this site the bryozoan *Hippothoa hyalina* was found encrusting the gastropods *Calyptrea fastigiata* and *Cerithiopsis* sp. The shells represent two different configurations; the former is hat-shaped and the latter is spiral-shaped. The bryozoan encrusting pattern for *Calyptrea* is similar to that of *Tegula* and the pattern for *Cerithiopsis* is similar to *Thais* and *Busycon*. The presence of the aforementioned gastropods as well as the pelecypods *Tresus* sp., *Saxidomus giganteus* and *Macoma* sp. indicates a low intertidal to subtidal environment. The bivalves, particularly *Tresus*, were articulated and indicate the absence of sediment reworking. The presence of these gastropods, as well as their probable hermit crab occupation, indicates that death and burial occurred at the site of the living components.

Ideally in order to test a null hypothesis that there is no difference between inhabited and non-inhabited shells, all shells would need to be collected at the same time of year. This was not possible because there are no unoccupied shells in summer, as indicated by the occupation of broken shells, whereas only empty shells were found in winter.

To test the hypothesis, a 2×2 contingency table was set up to measure the significance using chi-square with N as 1 degree of freedom. A chi-square value of 3.84 (1 degree of freedom or higher) indicates a 95% chance that the measured

association was not random, thereby nullifying the hypothesis (Simpson et al. 1960).

In comparing winter and summer collections of *Polinices duplicatus*, the chi-square was 4.7; *Thais haemostoma* collections had a chi-square of 13.3; results of *Busycon spiratum* and *B. contrarium* yielded no significant differences. In the case of the first two, the null hypothesis that there is no difference must be rejected as there is a difference between inhabited and non-inhabited shells. As the latter two do not yield the same results, it might be postulated that more robust shells or shells with thicker walls (i.e., *Polinices duplicatus*, *Thais haemostoma*) could survive in a relatively intact condition from summer to winter months while more delicate shells (i.e., *Busycon spiratum*, *B. contrarium*) would probably be lost. Therefore the shells *Polinices duplicatus*, *Thais haemostoma* were probably available for habitation late in the hermit crab season while both species of *Busycon* were available after the hermit crabs left the intertidal environment in winter.

The second null hypothesis to be tested is that there are no preferred settling areas on the hermit crab occupied shell. Tables 1 and 2 list five potential encrusting sites. Again a 2×2 contingency table was set up to measure the significance using chi-square with N as 1 degree of freedom with a correction for small sample size. In all the samples tested, there was no significant difference in selection of the inner surface, outer lip or inner lip (columella area). The values for the outer lip and bryozoan colony covering the shell varied from chi-square values of 2.194 to 2.4, or less than 75% but greater than 50% chance that the association was not random. In one instance (*Tegula funebris*, *Busycon spiratum*) there was less than 50% chance. The chi-square values for the inner lip (columella) and bryozoan colony covering the shell were 2.5 to 5.5, or greater than 75% but less than 99% chance.

The second null hypothesis figures are not as convincing in regards to preferential settling sites, but still indicate a greater than 50% chance that settling is not random with the hypothesis not well supported. It may be that all we can state is that there is a strong tendency for one site to be selected over another for encrustation.

Discussion

Results of the present study offer insights on several aspects of the biotic associations: crab and bryozoan behavior in selecting a shell or other substrate; factors possibly influencing bryozoan encrusting sites; and identification of hermit crab occupied shells in the fossil record.

Shell Availability

Hermit crab require a shell for protection from predation and environmental stress, as well as a place to brood their eggs (Back et al. 1976). If a hermit crab does not have a shell, it will not feed (Allee and Douglass 1945) and will subsequently die. In most environments suitable for hermit crabs, shells available for occupation are limited (Bertness 1981) because empty shells are rapidly broken up in the high energy environment. Hermit crabs will either occupy broken shells (Fotheringham 1976) or shells that are too small (Conover 1976, 1978). *Polinices* and *Thais* shells may survive into the winter but the more fragile *Busycon* shells would not.

Shell Alternatives

Some hermit crab species have found an alternative to occupying a suboptimal shell. The European species *Pagurus prideauxii* is found in association with the cloak anemone *Adamsia palliata*, and as the crab grows the anemone spreads itself like a cloak over the crab. In a west African association, the edge of the bryozoan colony extends over the aperture (Cook 1964) and thus serves to cover the crab as the crab grows.

Shell Preference

Hermit crabs were shown to prefer a clean shell over an encrusted shell if it is available (Grant and Ullmer 1974). Clean shells would be lighter in weight than heavily encrusted shells, but an eroded "second hand" shell, could be weakened by burrowing invertebrates or algae, or by abrasion.

Bryozoan larval Settlement

Bryozoans do not haphazardly select a substrate (Rogick and Croasdale 1949; Crisp 1973, 1974; Crisp and Ryland 1960; Ryland 1959, 1962, 1976; Pinter 1969; J. D. and D. F. Soule 1977; Cancino 1986). Clean substrate is first conditioned by the appearance of microflora (J. D. and D. F. Soule 1977); then if the substrate is unusually slippery or rough, the bryozoan can alter the substrate to a limited extent. Stebbing (1972) stated that a microbial surface flora could determine zones of favorability, at least on algal fronds. In species such as *Macrocytis* (giant brown kelp) which produce large amounts of mucus, it was noted that the area in front of the growing colony is altered with apparent mucus removal (Morris 1975). Bryozoans that encrust shells may etch the surface (Morris 1975) in an identifiable manner. Although J. Soule (1973) analyzed the bryozoan adhesive of several species, no worker has determined how the bryozoan cleans or etches the substrate.

Nutrient Availability: Particulate and Dissolved Organic Matter

If microbial surface flora could determine favorable encrusting zones in shells, then what factors would attract the microflora, at least on the inner surface of the upper lip of the gastropod shell occupied by a hermit crab? As the crab is tearing prey apart and feeding, or filtering out particulate matter, food debris could be lodged inside the shell along with fecal material, and amino acids would also be present (Ferguson 1982; Manahan 1983; Jaeckle 1985). These materials would offer nutrition to various microbial groups and to bryozoans. In studies on bryozoan nutrition (summarized by Ryland 1976; Best and Thorpe 1986a, b), it has been shown that bryozoans are capable of feeding on a variety of organic material. Net accumulation of amino acids by gymnolaemate bryozoans has been demonstrated by Stephens (1981).

It seems plausible then that bryozoans encrusting shells occupied by hermit crabs would tend to settle where an optimal concentration of food is available. As indicated in Tables 1, 2 and 3, as well as by the chi-square values discussed above, this is very likely to be on the inner surface of the outer lip or on the inner lip. A few bryozoans will settle elsewhere, although the variables which influence site selection are not entirely understood.

The Fossil Record

Hyden and Forest (1980) stated that hermit crabs are seldom preserved as fossils due to poor calcification as well as the delicate skeletal structure and the high energy environment in which they live. Although hermit crabs, as fossils, are known to exist at least from the Jurassic (Glaessner 1969), the record is sparse. Indications of hermit crab occupation by a bryozoan encrusted shell are as follows: development of hummocks or monticules on the bryozoan colony surface; multilaminar growth that surrounds the shell, but does not completely cover the aperture; and growth into the shell aperture [P. L. Cook formerly British Mus. (Nat. Hist.), pers. comm. and P. Taylor, British Mus. (Nat. Hist.), pers. comm.]. Palmer and Hancock (1973) noted characteristic flat areas on the shell and discontinuities in the bryozoan colonies due to the hermit crab dragging the shell. To this we add another factor, the position of the initial encrusting site, as an indication of hermit crab occupation.

Fossil shells that have been inhabited by hermit crabs may also serve in interpretation of paleoecology and stratigraphy. A fossil assemblage is not an intact community, due either to nonpreservation (Lawrence 1968) or transport. Hermit crabs modify shell assemblages by affecting the physical transport of the shell (Frey 1987). Identification of a shell as having been occupied by a hermit crab indicates a previously shallow water environment. Thus, even though the shell may have been transported to or from deeper waters, its final resting place could be considered shallow water if other associated fossil specimens also indicated the same conditions.

Symbiosis?

Are there, then, mutually beneficial effects of the association between bryozoans and hermit crabs? The bryozoan colonies, as they expand over the gastropod shell surface, might serve as camouflage. The preferential selection by hermit crabs of clean shells over shells containing epibiota mentioned above tends to negate the concept of a symbiotic relationship (Palmer and Hancock 1973) in which the bryozoans benefit the hermit crab by providing camouflage. The advantages for the bryozoans are more compelling; the sessile colonies become mobile, thereby providing them with protection from environmental changes in temperature, dissolved oxygen, and salinity, or from siltation. The association offers a suitable substrate with opportunities to reach new substrates for colonization. Bryozoans may feed on organic debris produced by the hermit crab in the form of fecal pellets, particles of food, microbiota, or dissolved organic matter. However, the limited number of bryozoan species found on hermit crab occupied shells indicates that they are restricted to those that can tolerate intermittent exposure to the air by the intertidal movements of the hermit crabs in exchange for the benefits provided.

Conclusions

There are distinctive differences in bryozoan settling patterns in hermit crab occupied shells and non-occupied shells. Results were statistically significant for *Polinices duplicatus* and *Thais haemostoma*, but not for the more fragile *Busycon* spp.

The hermit crab occupied shells of *Tegula funebris* in California were colonized exclusively by *Hippothoa hyalina* whereas Texas shells of *Polinices duplicata*, *Thais haemostoma* and *Busycon* spp. were inhabited exclusively by *Membranipora arborescens*, regardless of the presence of other epibiota. This further confirms the ability of certain bryozoan species to select preferred substrates.

Pattern of encrustation can be used to determine whether fossil or Recent shells were once inhabited by hermit crabs, indicating their shallow water habitat.

The benefits to the bryozoan species able to survive in the intertidal environment include access to a food supply, and mobility to protect from siltation or poor environmental conditions. The relationship is probably not symbiotic since predators are probably attracted to motion of the crabs rather than to the surface appearance. As discussed, the hermit crab will provide organic detritus and amino acids within the micro-habitat of the bryozoan in the apertural area of shell. These factors can be helpful to paleontologists in interpreting the fossil records.

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Seaweeds and Seagrasses of Southern California: Distributional Lists for Twenty-one Rocky Intertidal Sites

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Abstract.—A total of 213 macrophyte taxa was identified from 21 rocky intertidal sites in southern California, with 194 identified to the level of species, 14 to genus, and 5 to family. Eight southern California taxa were added to distributional records reported in the *Marine Algae of California*. The number of taxa ranged from 107 at Government Point, Santa Barbara County, to 51 at West Point, San Nicolas Island. No significant differences (Mann-Whitney two-sample test) in number of taxa were obtained between island and mainland or between sand-influenced and sand-free intertidal sites. Similarly, no significant difference (Kruskal-Wallis non-parametric ANOVA by ranks) was found in the numbers of taxa collected among sites exposed to warm, intermediate and cold water masses. It appears that site-specific combinations of environmental conditions determine species richness at southern California intertidal sites rather than large-scale patterns in abiotic environmental parameters.

Southern California coastal waters are characterized by a rich flora of benthic marine macroalgae and seagrasses. The relatively large coastal area, which includes a total of ca. 917 km of shoreline distributed over a latitudinal range of only ca. 212 km, exhibits much variation in exposure to wave action, ocean water masses, thermal regimes, and in substratum composition. This high degree of habitat heterogeneity is believed (Murray et al. 1980; see also Abbott and Hollenberg 1976) to contribute strongly to the high diversity of macrophytes known to occur in southern California waters.

Despite its taxonomic richness, knowledge of the southern California marine macrophyte flora is still best described as being in the early stages of exploration (see Murray 1974). Marine macroalgal floristics of southern California were advanced dramatically by Abbott and Hollenberg (1976) who provided taxonomic descriptions, distributional data and taxonomic keys for 669 species of California seaweeds. Unfortunately, little additional progress has been made in our taxonomic understanding of southern California seaweeds since Abbott and Hollenberg's (1976) classic work, and today floristic knowledge is poorly developed for most of the southern California region. This is particularly true for the seaweeds occurring on the relatively pristine and biogeographically important Southern California Islands where taxonomic contributions during the last 12 years have been limited to species lists provided with ecological (Littler 1979) and geographical (Apt et al. 1988) surveys. This situation contrasts greatly, for example, with

the considerable progress that has been made (e.g., Scagel et al. 1986; Gabrielson et al. 1987) in advancing our understanding of the systematics of the seaweeds of northern Washington, British Columbia and southeast Alaska.

This paper provides lists of marine macroalgae and seagrasses collected from 21 southern California intertidal sites during the 1975–1979 ecological sampling program sponsored by the U.S. Department of Interior, Bureau of Land Management (now referred to as Minerals Management Services). Previous versions of these records have been used for distributional analyses of macrophytes occurring in southern California waters (Murray et al. 1980; Murray and Littler 1981). However, the species lists generated for these sites are currently available only in unpublished governmental reports. These distributional data for intertidal seaweeds and seagrasses are of particular value considering the paucity of recent floristic information on southern California macrophytes.

Methods

Marine macroalgae and seagrasses were collected from 21 rocky intertidal sites located in southern California between Point Conception and the United States-Mexico border (Fig. 1; Table 1). Seven stations were located on the mainland and 14 were established on the eight Southern California Islands or Channel Islands which have been divided (Philbrick 1967) into Northern (San Miguel, Santa Rosa, Santa Cruz, and Anacapa) and Southern (San Nicolas, Santa Barbara, Santa Catalina, and San Clemente) groups. A minimum of one station was established on each island, with seven stations located on members of the Northern and seven on members of the Southern Channel Island groups.

Study sites encompassed the geographic extent of the southern California region and consisted of areas representative of protected or semi-protected rocky shoreline. Collections were not made at sites that received consistently heavy wave action, such as characterizes much of the central and northern California coast (see Ricketts et al. 1985) which receives direct exposure to ocean swells. Similarly, sites varied as to the composition and stability of the substratum, and exposure to ocean currents and seawater temperature regimes.

The study sites (Fig. 1; Table 1) were visited from one to several times between July 1975 and July 1979. Macrophyte collections at each site were made over a period of at least three days and included not only taxa found in ecological samples, but also specimens of conspicuous forms observed in the vicinity of the study areas. Details of the ecological sampling program including the visitation dates for each site are provided elsewhere (Littler 1977, 1978, 1979, 1980a, b; Littler and Littler 1985) and, hence, will not be described here.

Because only 12 of the 21 study sites were sampled throughout the year (summer, fall, winter, spring), seasonally-occurring macrophyte taxa were likely missed at the sites subjected to less intense seasonal sampling. Our observations at the 12 sites where seasonal sampling occurred suggest that relatively few intertidal macrophytes are completely absent from the southern California shoreline during any particular season. However, we did record significantly fewer numbers of taxa at the 9 sites subjected to incomplete seasonal sampling (Crook Harbor, San Miguel Island; Prisoner's Harbor, Santa Cruz Island; South Coast and North Coast, Anacapa Island; West Point, San Nicolas Island; Catalina Harbor, Santa Catalina Island; Northwest Coast, San Clemente Island; Paradise Cove, Los Angeles Coun-

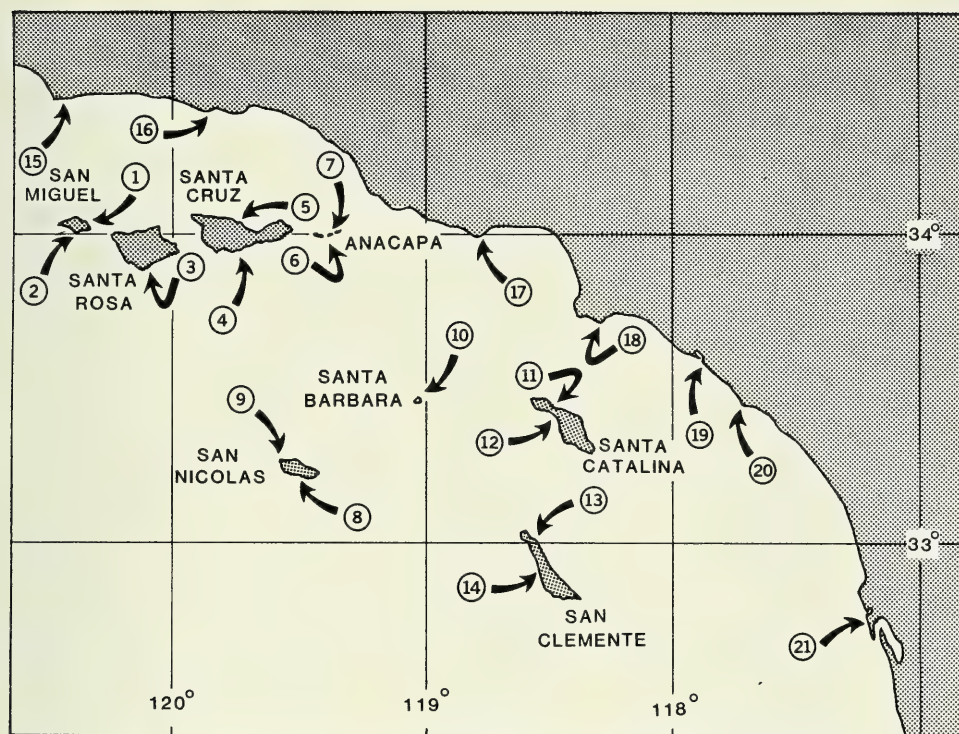


Fig. 1. Locations of the 21 rocky intertidal sites. Refer to Table 1 for numerical key to sites.

ty; and, Dana Point, Orange County) compared with the 12 sites where collections were made throughout the year (65.0 ± 9.4 vs. 84.8 ± 13.8 S.D.; Mann-Whitney two-sample test, $U = 94.0$, $n_1 = 12$, $n_2 = 9$, $P < .01$). Analyses of taxa numbers using only data from the 12 sites where seasonal sampling was performed produced statistical results identical to those where all 21 sites were considered. Consequently, the numbers of taxa reported herein and employed in statistical comparisons are the "raw" recorded values and have not been weighted to reflect sampling frequency.

Macrophyte collections generally were preserved in 3–5% Formalin-seawater as suggested by Abbott and Tsuda (1985) and returned to the laboratory for identification and processing. Specimens were identified by the authors; most identifications were confirmed by Dr. Isabella A. Abbott, currently of the University of Hawaii. For selected macrophytes such as crustose algae and members of taxonomically difficult genera (e.g., *Cladophora*, *Ceramium*, and *Polysiphonia*), identification to the species level usually was not performed due to time constraints. Instead these specimens have been categorized under higher taxonomic units, i.e., genus or family. Herbarium specimens of most taxa were prepared and deposited in the U.S. National Herbarium, National Museum of Natural History, Smithsonian Institution.

Results

A total of 213 taxa was identified from the 21 rocky intertidal sites, with 194 identified to the species level, 14 to the level of genus and 5 to the level of family. A list of the taxa and the sites at which they were collected is presented in Table 2.

Table 1. Names, locations, characteristics, and numbers of taxa for the 21 rocky intertidal sites. Floristic affinities are derived from Murray and Littler (1981).

Site number	Site location	Latitude and longitude	Floristic affinity	Sand or cobble influence	Number of taxa
Island sites					
1	San Miguel Island, Cuyler Harbor	34°02'55"N 120°20'08"W	cold	yes	85
2	San Miguel Island, Crook Point	34°01'28"N 120°22'43"W	cold	no	62
3	Santa Rosa Island, South Point	33°53'31"N 120°06'31"W	cold	yes	78
4	Santa Cruz Island, Willows Anchorage	33°57'43"N 119°45'16"W	intermediate	no	89
5	Santa Cruz Island, Prisoners Cove	34°01'14"N 119°41'14"W	intermediate	no	61
6	Anacapa Island, South Coast	34°00'19"N 119°25'05"W and 34°00'24"N 119°24'38"W	warm	no	77
7	Anacapa Island, North Coast	34°00'31"N 119°24'21"W	warm	no	58
8	San Nicolas Island, Dutch Harbor	33°12'54"N 119°28'22"W	cold	yes	98
9	San Nicolas Island, West Point	33°16'43"N 119°34'41"W	cold	no	51
10	Santa Barbara Island, Cave Canyon	33°28'43"N 119°01'36"W	intermediate	no	92
11	Santa Catalina Island, Fisherman Cove	33°26'47"N 118°29'04"W	warm	no	91
12	Santa Catalina Island, Catalina Harbor	33°25'42"N 118°30'42"W	warm	no	69
13	San Clemente Island, Wilson Cove	33°00'06"N 118°33'03"W	warm	no	79
14	San Clemente Island, Northwest Coast	33°58'06"N 118°34'18"W	warm	no	80
Mainland sites					
15	Government Point, Santa Barbara County	34°26'35"N 120°27'06"W	cold	yes	107
16	Coal Oil Point, Santa Barbara County	34°24'27"N 119°52'40"W	intermediate	yes	95
17	Paradise Cove (Malibu), Los Angeles County	34°00'42"N 118°47'30"W	intermediate	yes	68
18	Whites Point, Los Angeles County	33°43'11"N 118°19'39"W	warm	yes	58
19	Corona Del Mar, Orange County	33°35'14"N 117°51'54"W	warm	yes	65
20	Dana Point, Orange County	33°35'25"N 117°42'44"W	warm	yes	59
21	Ocean Beach, San Diego County	32°44'35"N 117°15'15"W	warm	no	80

Table 2. Lists of macroalgal and seagrass taxa for the 21 rocky intertidal stations. Nomenclature after Abbott and Hollenberg (1976) as modified by Scagel et al. (1986).

Taxon	Site number
Division Chlorophyta	
O. Ulotrichales	
f. Chaetophoraceae	
unidentified crust	9
f. Monostromataceae	
Monostroma zostericola Tild.	15
f. Ulvaceae	
Enteromorpha spp.	
Enteromorpha clathrata var. clathrata (Roth) Grev.	5, 7, 8, 9, 10, 11, 12, 13, 14, 16, 18, 19, 21
Enteromorpha compressa (L.) Grev.	10, 13, 15, 16
Enteromorpha flexuosa (Roth) J. Ag.	5, 13
Enteromorpha intestinalis (L.) Link	1, 2, 4, 8, 16, 21
Enteromorpha linza (L.) J. Ag.	1, 3, 8, 17, 21
Ulva angusta S. & G.	8, 21
Ulva californica Wille	16
Ulva lobata (Kütz.) S. & G.	1, 2, 4, 5, 6, 7, 11, 12, 13, 17, 18, 19, 20, 21
Ulva taeniata (Setch.) S. & G.	1, 2, 3, 4, 5, 8, 9, 10, 14, 15, 16
O. Cladophorales	
f. Cladophoraceae	
Chaetomorpha linum (Müll) Kütz.	1, 2, 3, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21
Chaetomorpha spiralis Okam.	4, 21
Cladophora spp.	1, 2, 3, 4, 6, 7, 8, 10, 11, 12, 13, 14, 15, 16, 18, 19, 21
Cladophora columbiana Coll.	1, 2, 3, 4, 6, 8, 9, 15, 17, 21
Cladophora sakaii Abb.	16
O. Siphonocladales	
f. Siphonocladaceae	
Cladophoropsis fasciculatus (Kjellm.) Okam.	1, 8, 11, 13

Table 2. Continued.

Taxon	Site number
O. Codiales	
f. Bryopsidaceae	
Bryopsis corticulans Setch.	1, 4, 6, 8, 9, 10, 11, 15, 16, 18, 19, 21
f. Derbesiaceae	
Derbesia marina (Lyngb.) Sol.	10
f. Codiaceae	
Codium cuneatum S. & G.	11, 12
Codium fragile (Sur.) Har.	1, 2, 3, 4, 6, 8, 9, 10, 11, 12, 13, 14, 15, 17, 19, 20
Codium hubbsii Daws.	10, 11, 14
Codium setchellii Gardn.	1, 2, 10, 11, 15
Division Phaeophyta	
O. Ectocarpales	
f. Ectocarpaceae	
unidentified filamentous species	3, 4, 5, 6, 7, 8, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21
O. Chordariales	
f. Ralfsiaceae	
unidentified encrusting species	1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21
Diplura simulans Hollenb.	10
Hapalospongion gelatinosum Saund.	6, 12, 21
Hapterophycus canaliculatus S. & G.	4, 10, 11, 12
Pseudolithoderma nigra Hollenb.	2, 4, 6, 7, 10, 11, 12, 13, 14
f. Corynophlacaceae	
Cylindrocarpus rugosus Okam.	1, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21
Leathesia nana S. & G.	8, 15
f. Chordariaceae	
Anapilus japonicus (Harv.) Wynne	15
Haplogloia andersonii (Farl.) Levr.	15

Table 2. Continued.

Taxon	Site number
O. Dictyosiphonales	
f. Dictyosiphonaceae	
Coilodesme rigida S. & G.	13
f. Punctariaceae	
Soranthera ulvoidea Post. & Rupr.	15
O. Scytosiphonales	
f. Scytosiphonaceae	
Colpomenia peregrina (Sauv.) Ham. and Colpomenia sinuosa (Roth) Derb. & Sol.	3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21 3, 4, 6, 10, 11, 12, 13, 14, 15, 17, 20, 21 11, 13
Endarachne binghamiae J. Ag.	2, 4, 6, 10, 11, 15, 16, 17, 18
Hydroclathrus clathratus (C. Ag.) Howe	1, 3, 5, 6, 7, 10, 11, 13, 14, 15, 16, 17, 19, 21
Petalonia fascia (Müll.) Kuntze	3, 4, 8, 9, 11, 12, 13, 15, 16, 17, 18, 19, 21
Scytosiphon dotyi Wynne	
Scytosiphon lomentaria (Lyngb.) J. Ag.	
O. Dictyotales	
f. Dictyotaceae	
Dictyopteris johnstonei Gardn.	4, 6, 10
Dictyopteris undulata Holmes	4, 9, 10, 11, 13, 19, 21
Dictyota flabellata (Coll.) S. & G.	4, 7, 9, 10, 11, 12, 13, 14, 16, 17, 18, 19, 20, 21
Pachydictyon coriaceum (Holmes) Okam.	4, 6, 10, 11, 12, 13, 14, 16, 17, 18, 19, 20, 21
Taonia lennebackeriae J. Ag.	3, 8, 16
Zonaria farlowii S. & G.	4, 6, 7, 11, 12, 13, 14, 16, 17, 20
O. Sphacelariales	
f. Sphacelariaceae	
Sphacelaria californica (Sauv.) S. & G.	7, 12, 13
Sphacelaria furcigera Kütz.	6, 7, 11

Table 2. Continued.

Taxon	Site number
O. Desmarestiales	
f. Desmarestiaceae	
<i>Desmarestia ligulata</i> var. <i>ligulata</i> (Lightf.) Lamour.	3, 4, 5, 8, 10, 14, 15
O. Laminariales	
f. Laminariaceae	
<i>Laminaria</i> sp.	8
<i>Laminaria farlowii</i> Setch.	5, 7
<i>Laminaria setchellii</i> Silva	1, 2, 9
<i>Laminaria sinclairii</i> (Harv.) Farl., Anders. & Eaton	15
f. Alariaceae	
<i>Egregia menziesii</i> (Turn.) Aresch.	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21
<i>Eisenia arborea</i> Aresch.	4, 6, 7, 8, 9, 10, 11, 12, 13, 19, 20
f. Lessoniaceae	
<i>Macrocystis pyrifera</i> (L.) C. Ag.	3, 4, 5, 6, 8, 9, 10, 11, 13, 16, 17, 19
O. Fucales	
f. Fucaceae	
<i>Fucus gardneri</i> Silv.	15
<i>Hesperophycus harveyanus</i> (Decne.) S. & G.	1, 2, 3, 4, 6, 7, 8, 11, 12, 14, 15, 19
<i>Pelvetia fastigiata</i> f. <i>fastigiata</i> (J. Ag.) DeToni	15, 16, 17, 19, 20
<i>Pelvetia fastigiata</i> f. <i>gracilis</i> S. & G.	1, 2, 3, 4, 5, 6, 7, 8, 9, 11, 12, 13, 14
f. Cystoseiraceae	
<i>Cystoseira neglecta</i> S. & G.	11, 20
<i>Cystoseira osmundacea</i> (Turn.) C. Ag.	4, 7, 16, 17, 18
<i>Cystoseira setchellii</i> Gardn.	7
<i>Halidrys dioica</i> Gardn.	2, 3, 4, 6, 8, 9, 10, 11, 12, 13, 14, 15, 16, 19, 20
f. Sargassaceae	
<i>Sargassum agardhianum</i> J. Ag.	10, 11, 12, 13, 14, 20
<i>Sargassum muticum</i> (Yendo) Fensh.	5, 7, 11, 12, 13, 14, 18, 19, 20

Table 2. Continued.

Taxon	Site number
Division Rhodophyta	
O. Bangiales	
f. Erythropeltidaceae	
Erythrotrichea carnea (Dillw.) J. Ag.	19
Smithora naiadum (Anders.) Hollenb.	1, 3, 5, 6, 8, 15, 16, 17, 21
f. Bangiaceae	
Bangia vermicularis Harv.	1, 4
Porphyra lanceolata (Setch. & Hus) Smith	1, 2
Porphyra perforata J. Ag.	1, 2, 3, 4, 5, 6, 8, 10, 14, 15, 16, 18, 19, 21
Porphyra thuretii Daws.	15
Porphyrella californica Hollenb.	11, 12, 13
O. Nemaliales	
f. Acrochaetiaceae	
Audouinella daviesii (Dillw.) Woelk.	11
f. Nemaliaceae	
Nemalion helminthoides (Vell.) Batt.	1, 2, 3, 4, 5, 6, 8, 10, 11, 12, 13, 14, 16, 17, 18, 21
f. Helminthocladiaceae	
Cumagloia andersonii (Farl.) S. & G.	4, 10, 17, 18, 21
f. Bonnemaisoniaceae	
Bonnemaisonia hamifera Har.	14
f. Gelidiaceae	
Gelidium coulteri Harv. and Gelidium pusillum (Stackh.) LeJolis	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21
Gelidium nudifrons Gardn.	7, 13, 15
Gelidium purpurascens Gardn.	1, 4, 5, 6, 7, 10, 11, 12, 13, 14, 15, 16, 17, 19, 21
Gelidium robustum (Gardn.) Hollenb. & Abb.	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21
Pterocladia capillacea (Gmel.) Born. & Thur.	1, 3, 4, 5, 6, 7, 8, 10, 11, 12, 13, 14, 16, 17, 18, 19, 20, 21
Pterocladia media Daws.	6, 12, 14, 16

Table 2. Continued.

Taxon	Site number
<i>O. Cryptonemiales</i>	
f. Dumontiaceae	10
Farlowia mollis (Harv. & Bail.) Farl. & Setch.	14, 15
Pikea californica Harv.	
f. Peyssonelliaceae and Hildenbrandiaceae	1, 2, 3, 4, 5, 6, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21
unidentified crusts	
f. Corallinaceae	
Amphiroa zonata Yendo	4, 10, 11, 12, 19
Bossiella orbigniana ssp. dichotoma (Manza) Johansen	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21
Bossiella orbigniana ssp. orbigniana (Dec.) Silva	6, 7, 10, 11, 16, 18, 19, 20
Calliarthron cheilosporioides Manza	1, 2, 9, 17
Calliarthron tuberculosum (Post. & Rupr.) Daws.	1, 3, 4, 6, 8, 9, 10, 11, 15, 16, 19
Corallina officinalis var. chilensis (Dec.) Kütz.	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21
Corallina vancouveriensis Yendo	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21
Haliptylon gracile (Lamour.) Johans.	1, 6, 7, 10, 11, 12, 13, 14, 19, 20, 21
Jania crassa Lamour.	6, 10, 14, 20, 21
Jania tenella (Kütz.) Grun.	11, 12, 13, 14
Lithothrix aspergillum Gray	3, 4, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21
Melobesia medioeris (Fosl.) Setch. et Mason	1, 2, 3, 4, 5, 6, 8, 13, 15, 16, 17, 20, 21
unidentified crustose species	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17
f. Gloiosiphoniaceae	
Gloiosiphonia capillaris (Huds.) Berk.	3, 15
Schimmelmania plumosa (Setch.) Abb.	15
f. Endocodiaceae	
Endocladia muricata (Post. & Rupr.) J. Ag.	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 14, 15, 16, 17
Glotopeltis furcata (Post. & Rupr.) J. Ag.	11, 12
f. Cryptonemiaceae	
Carpopeltis bushiae (Farl.) Kyl.	10
Carpopeltis divaricata Okam.	5, 6, 8, 11, 12, 13

Table 2. Continued.

Taxon		Site number
<i>Grateloupia doryphora</i> (Mont.) Howe		1, 2, 3, 4, 5, 8, 10, 14, 15, 16, 17, 21
<i>Grateloupia</i> sp.		4
<i>Prionitis angusta</i> (Harv.) Okam.		10, 12
<i>Prionitis cornea</i> (Okam.) Daws.		3, 20
<i>Prionitis lanceolata</i> (Harv.) Harv.		1, 3, 4, 5, 6, 7, 8, 9, 10, 15, 16, 17, 18
<i>Prionitis linearis</i> Kyl.		17
f. <i>Kallymeniaceae</i>		
<i>Callophyllis flabellulata</i> Harv.		19, 21
<i>Callophyllis violacea</i> J. Ag.		1, 2, 3, 8, 10, 15, 16
<i>Callophyllis</i> sp.		10, 15
O. Gigartinales		
f. <i>Petrocelidaceae</i>		
<i>Petrocelis middendorffii</i> (S. & G.) West		1, 2, 4, 9, 15, 18
f. <i>Nemastomataceae</i>		
<i>Schizymenia pacifica</i> (Kyl.) Kyl.		3, 5, 6, 10, 13, 15, 21
f. <i>Solieriaceae</i>		
<i>Opuntia californica</i> (Farl.) Kyl.		18
<i>Sarcodiotheca gaudichaudii</i> (Mont.) Gabr.		1, 2, 4, 8, 10, 15, 16, 17
<i>Sarcodiotheca furcata</i> (S. & G.) Kyl.		8
f. <i>Hypneaceae</i>		
<i>Hypnea johnstonii</i> S. & G.		11
<i>Hypnea valentiae</i> var. <i>valentiae</i> (Turn.) Mont.		7, 11, 14, 20, 21
f. <i>Plocamiaceae</i>		
<i>Plocamium cartilagineum</i> (L.) Dix.		1, 2, 3, 6, 8, 10, 11, 12, 13, 14, 15, 16, 17, 20, 21
<i>Plocamium violaceum</i> Farl.		1, 2, 3, 4, 8, 10, 11, 15, 19, 21
f. <i>Gracilariaceae</i>		
<i>Gracilaria lemaneiformis</i> (Bory) Weber-van Bosse		15

Table 2. Continued.

Taxon	Site number
Gracilaria pacifica Abb.	1, 2, 8, 11, 16
Gracilaria papenfussii Abb.	4, 16
f. Phyllophoraceae	
Ahnfeltia gigartinoides J. Ag.	15
Ahnfeltia plicata (Huds.) Fries	1, 15
Besla papillaeformis Setch.	9
Gymnogongrus chiton (Howe) Silv. et DeCew	5, 8, 15
Gymnogongrus leptophyllus J. Ag.	1, 2, 8, 14, 15, 16, 17, 20
Stenogramme interrupta (C. Ag.) Mont.	1, 2, 8, 16
f. Gigartinaceae	
Gigartina canaliculata Harv.	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21
Gigartina corymbifera (Kütz.) J. Ag.	1, 2, 8, 15
Gigartina exasperata Harv. & Bail.	8, 15
Gigartina harveyana (Kütz.) S. & G.	1, 2, 4, 7, 8, 15, 16
Gigartina leptorhynchos J. Ag.	3, 4, 5, 6, 7, 8, 9, 15, 16, 18
Gigartina spinosa (Kütz.) Harv.	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 20, 21
Gigartina volans (C. Ag.) J. Ag.	2, 3, 8, 15, 16
Iridaea cordata var. cordata (Turn.) Bory	1, 2, 3, 4, 8, 9, 10, 15, 16
Iridaea heterocarpa Post. & Rupr.	1, 3, 8, 15
Iridaea lineare (S. & G.) Kyl.	15
Mastocarpus jardinii (J. Ag.) West	1, 8, 15
Mastocarpus papillatus (C. Ag.) Kütz.	1, 2, 3, 4, 5, 6, 7, 8, 9, 15, 16, 18
Rhodoglossum affine (Harv.) Kyl.	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21
Rhodoglossum californicum (J. Ag.) Abb.	8
O. Rhodymeniales	
f. Rhodymeniaceae	
Botryocladia pseudodichotoma (Eart.) Kyl.	8
Rhodymenia californica var. californica Kyl.	3, 4, 5, 6, 7, 8, 10, 11, 12, 13, 14, 15, 16, 18, 19, 20, 21
Rhodymenia pacifica Kyl.	1, 4, 5, 6, 10, 15, 17

Table 2. Continued.

Taxon	Site number
f. Champiaceae	
<i>Coeloseira compressa</i> Hollenb.	3, 6, 7, 19
<i>Gastroclonium subarticulatum</i> (Turn.) Kütz.	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 13, 14, 15, 16, 17, 18, 19, 20, 21
O. Ceramiales	
f. Ceramiaceae	
<i>Callithamnion pikeanum</i> Harv.	1, 2, 3, 8, 15, 16
<i>Callithamnion rupicolum</i> Anders.	1, 2, 3, 4, 6, 8, 9, 11, 12, 13, 14, 15, 16, 18, 21
<i>Callithamnion</i> spp.	3, 6, 7, 8
<i>Centroceras clavulatum</i> (C. Ag.) Mont.	1, 2, 3, 6, 7, 8, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21
<i>Ceramium codicola</i> J. Ag.	4, 10, 11, 19, 20
<i>Ceramium eatonianum</i> (Farl.) DeToni & <i>Ceramium sinicola</i> S. & G.	1, 2, 3, 4, 5, 6, 7, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21
<i>Ceramium pacificum</i> (Coll.) Kyl.	3, 8
<i>Ceramium viscainoense</i> Daws.	4, 10, 18, 21
<i>Ceramium</i> spp.	1, 3, 4, 5, 6, 8, 10, 11, 12, 13, 14, 18, 19, 20, 21
<i>Microcladia borealis</i> Rupr.	1, 2, 15
<i>Microcladia californica</i> Farl.	13, 15
<i>Microcladia coulteri</i> Harv.	1, 2, 3, 4, 5, 8, 10, 15, 16, 17
<i>Platythamnion heteromorphum</i> (J. Ag.) J. Ag.	15
<i>Pleonosporium squarulosum</i> (Harv.) Abb.	1, 16, 17
<i>Tiffaniella snyderiae</i> (Farl.) Abb.	1, 5, 8, 11, 13, 14, 15, 16, 17, 18, 21
f. Delesseriaceae	
<i>Acrosorium uncinatum</i> (Turn.) Kyl.	5, 10, 11, 13, 14, 16, 18, 19, 20, 21
<i>Anisocladella pacifica</i> Kyl.	1, 8, 10, 11, 13, 15, 16, 17, 19, 21
<i>Cryptopleura corallinara</i> (Nott.) Gardn.	10, 11, 12, 13, 18, 20, 21
<i>Cryptopleura crispa</i> Kyl.	1, 3, 4, 5, 6, 7, 8, 10, 13, 14, 15, 16, 17, 18, 19, 20, 21
<i>Cryptopleura lobulifera</i> (J. Ag.) Kyl.	2, 3, 4, 21
<i>Cryptopleura ruprectiana</i> (J. Ag.) Kyl.	1, 2, 15
<i>Cryptopleura violacea</i> (J. Ag.) Kyl.	1, 2, 8, 9, 10, 15, 16
<i>Hymenena flabelligera</i> (J. Ag.) Kyl.	8
<i>Nienburgia andersoniana</i> (J. Ag.) Kyl.	5, 6, 8, 14, 15, 16, 19, 21
<i>Phycodrys setchellii</i> Skottsb.	1, 3, 5, 15, 16, 17

Table 2. Continued.

Taxon	Site number
f. <i>Dasyaceae</i>	
<i>Heterosiphonia erecta</i> Gardn.	13, 14, 21
<i>Pogonophorella californica</i> (J. Ag.) Silv.	3, 8, 15, 16, 21
<i>Dasya</i> sp.	14
f. <i>Rhodomelaceae</i>	
<i>Chondria arcuata</i> Hollenb.	6
<i>Chondria californica</i> (Coll.) Kyl.	4, 5, 7, 11, 12, 14, 16, 18, 19, 20, 21
<i>Chondria decipiens</i> Kyl.	8, 14, 15, 16, 20
<i>Chondria nidifica</i> Harv.	1, 8, 15, 16, 17
<i>Chondria</i> sp.	3
<i>Erythrocytis saccata</i> (J. Ag.) Silv.	4, 5, 9, 10, 11, 16, 17, 19, 20
<i>Herposiphonia littoralis</i> Hollenb.	4, 6, 7, 11, 12, 13, 14, 18, 19, 20, 21
<i>Herposiphonia plumula</i> (J. Ag.) Hollenb.	1, 3, 4, 7, 8, 10, 11, 13, 14, 16, 17, 18, 19, 20
<i>Herposiphonia verticillata</i> (Harv.) Kyl.	1, 3, 4, 10, 12, 13, 14, 18, 21
<i>Laurencia masonii</i> S. & G.	4, 6, 12, 13, 18, 20
<i>Laurencia pacifica</i> Kyl.	4, 5, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 19, 20, 21
<i>Laurencia sinicola</i> S. & G.	3, 4, 5, 6, 7, 9, 10, 11, 12, 13, 14, 17, 18, 19, 20, 21
<i>Laurencia snyderiae</i> Daws.	11, 13, 14
<i>Laurencia spectabilis</i> Post. & Rupr.	1, 2, 3, 4, 5, 6, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17
<i>Laurencia splendens</i> Hollenb.	1, 2, 4, 8, 11, 15, 16
<i>Laurencia subopposita</i> (J. Ag.) Setch.	11, 14, 16, 17, 21
<i>Laurencia</i> sp.	3, 21
<i>Neorhodomela larix</i> (Turn.) Masuda	15
<i>Ophiodocladus simpliciusculus</i> (Crouan & Crouan) Falk.	21
<i>Polysiphonia acuminata</i> Gardn.	4, 6, 8, 10, 11, 12, 14, 15, 16, 17, 19, 21
<i>Polysiphonia hendryi</i> var. <i>hendryi</i> Gardn.	1, 2, 3, 4, 5, 7, 8, 9, 10, 11, 12, 14, 15, 16, 17, 18, 20, 21
<i>Polysiphonia johnstonii</i> S. & G.	16
<i>Polysiphonia pacifica</i> Hollenb.	1, 16
<i>Polysiphonia paniculata</i> Mont.	1, 8, 15
<i>Polysiphonia scopulorum</i> var. <i>villum</i> (J. Ag.) Hollenb.	1, 6, 7, 9, 10, 11, 12, 13, 14, 15, 16, 18
<i>Polysiphonia</i> spp.	2, 3, 4, 5, 6, 8, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 21

Table 2. Continued.

Taxon	Site number
Pterosiphonia baileyi (Harv.) Falk.	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 13, 14, 15, 16, 19, 21
Pterosiphonia bipinnata (Post. & Rupr.) Falk.	8, 15
Pterosiphonia dendroidea (Mont.) Falk.	1, 3, 4, 5, 6, 7, 8, 10, 11, 13, 14, 15, 16, 17, 18, 19, 20, 21
Pterosiphonia pennata (C. Ag.) Falk.	11, 12, 14, 15
Division Spermatophyta	
f. Zosteraceae	
Phyllospadix scouleri Hook	1, 3, 4, 5, 8, 9, 10, 14, 15
Phyllospadix torreyi Wats.	2, 3, 6, 7, 8, 11, 12, 13, 15, 16, 17, 19, 20, 21

The number of taxa identified for each station varied from 107 (Government Point, Santa Barbara County) to 51 (West Point, San Nicolas Island) and averaged 76.3 ± 15.5 S.D.; no particular relationship between the number of species collected and the main abiotic features of the sites were apparent. Statistically significant differences were not obtained either between island and mainland (76.4 ± 14.3 vs. 76.0 ± 18.9 ; Mann-Whitney two-sample test, $U = 51.0$, $n_1 = 14$, $n_2 = 7$, $P > .05$) or between sites characterized (see Murray et al. 1980; Murray and Littler 1981) as exposed to water masses of warm (71.6 ± 11.5), cold (80.2 ± 21.2) and intermediate (81.0 ± 15.4) seawater temperatures (Kruskal-Wallis nonparametric ANOVA by ranks, $H = 1.85$, $df = 2$, $P = 0.60$). Similarly, no significant difference in numbers of taxa was obtained (Mann-Whitney two-sample test, $U = 62.5$, $n_1 = 9$, $n_2 = 12$, $P > .05$) when comparisons were made between sites identified (Littler et al. 1989) as mostly receiving exposure to seasonal sand inundation or cobble movements (79.2 ± 18.0) and those essentially free of sand or cobble influence (74.1 ± 13.7).

Discussion

The results of this study significantly augment existing distributional records of southern California macrophytes by providing lists of intertidal floras for 14 island and 7 mainland sites. Although floral lists for numerous southern California mainland sites exist (e.g., Dawson 1959, 1965; Widdowson 1971; Nicholson and Cimberg 1971; Thom and Widdowson 1978; Thom 1980), prior to our study intertidal floras of island stations were known for only San Clemente (Sims 1974; Littler and Murray 1975; Murray and Littler 1977), Santa Cruz (Seapy and Littler 1982; Apt et al. 1988) and San Nicolas (Caplan and Boolootian 1967; Littler et al. 1983) Islands. Additionally, this study adds eight new taxa (specimens are on file at the National Herbarium) to the list of algae known to occur in southern California waters based on distributional data provided by Abbott and Hollenberg (1976). Two of these (*Ceramium viscainoense* and *Carpopeltis divaricata*) are not listed for the California flora by Abbott and Hollenberg (1976), but appear in a list of algae collected from Santa Cruz Island (Apt et al. 1988). They represent species that appear to have more southerly distributions. Each of the remaining six taxa (*Besapapillaeformis*, *Hymenena flabelligera*, *Mastocarpus jardinii*, *Microcladia borealis*, *Monostroma zostericola*, and *Porphyra lanceolata*) are species with more northerly, cold water distributional centers. These species appear in southern California waters at sites most proximal to the colder waters of the California Current, i.e., on San Miguel and San Nicolas Islands or at Government Point. With the exception of *Porphyra lanceolata*, which was found in southern California waters by Nicholson and Cimberg (1971), none of these taxa has appeared in recent species lists (e.g., Widdowson 1971; Thom and Widdowson 1978; Thom 1980; Apt et al. 1988) of southern California intertidal seaweeds.

Prior to our research, few studies of intertidal algae on the relatively isolated offshore islands had been performed (see Murray 1974). Consequently, we anticipated that our study, besides providing new, site-specific lists, would result in numerous additions to the southern California flora and perhaps, several new species. Although we generated new distributional records for individual islands, our sampling program produced only eight additions to Abbott and Hollenberg's (1976) list of species occurring in southern California waters. This suggests that

the list of intertidal macrophytes comprising the southern California flora likely will expand only after careful biosystematic study. However, it is probable that many species as yet unreported for southern California waters, particularly those with distributional centers north of Point Conception, eventually will be identified from subtidal habitats in southern California. Stewart (1984) has observed that several species common in the low intertidal zone along central California shores occur in deep subtidal sites in southern California, indicating that colder water seaweeds can survive at more southerly latitudes by occupying deeper water habitats. Her observations are supported by Lewbel et al. (1981) who found that the shallow subtidal (ca. 20 m) fauna and flora of Cortes and Tanner Banks, two seamounts located ca. 180 km west of San Diego, had close affinity with the cold water, central California biota.

In examining the distributions provided in Table 2, in conjunction with our own observations and information provided by Abbott and Hollenberg (1976) and Abbott and North (1972), it is possible to identify seaweeds that serve as potential indicators of cold or warm water intertidal habitats in southern California. Cold water sites, such as those at Government Point and on San Nicolas and San Miguel Islands, appear to support populations of seaweeds such as *Analipus japonica*, *Fucus gardneri*, *Laminaria setchellii*, *Callithamnion pikeanum*, *Iridaea cordata* var. *cordata*, *Neorhodomela larix*, and *Laurencia spectabilis*. In contrast, intertidal habitats of sites characterized by exposure to warm water masses, such as occur for much of Santa Catalina and San Clemente Island, are often uniquely characterized by populations of *Colpomenia sinuosa*, *Dictyopteris undulata*, *Eisenia arborea*, *Endarachne binghamiae*, *Halidrys dioica*, *Sargassum agardhi-anum*, *Zonaria farlowii*, *Chondria californica*, *Jania tenella*, *Laurencia snyderiae*, and *Pterocladia capillacea*.

The abiotic environmental features of greatest importance in determining the abundances of macrophyte populations and the structure of macrophyte communities in southern California intertidal habitats appear to be the frequency and extent of sand scouring and accumulation on the rocky substratum, and the thermal characteristics of the water masses to which a site is exposed (Littler, et al. 1989). However, our analyses indicate that there is no relationship between species richness and the thermal regime or the degree of sand influence for intertidal sites in southern California. Additionally, species richness does not vary significantly between island and mainland sites. These findings suggest that the richness of rocky intertidal macrophyte floras in southern California is controlled by site-specific factors and does not conform to patterns based on large-scale gradients of abiotic environmental features or insular geographical position.

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A New Species of Early Pleistocene Cotton Rat from the Anza-Borrego Desert of Southern California

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Abstract.—Fossil cotton rats, genus *Sigmodon*, were recovered from the superposed Vallecito-Fish Creek beds of the Palm Spring Fm. in Anza-Borrego State Park, California. *Sigmodon minor* is the common cotton rat species throughout the late Pliocene Layer Cake and Arroyo Seco faunal intervals. A new species, *S. lindsayi*, characterized by large size and a suite of features of the first lower molar, appears first in the early Pleistocene Vallecito Creek faunal interval, extending from collecting zone 53.8 to zone 58.8, from approximately 610 to 305 meters from the top of the sequence. *Sigmodon lindsayi* is replaced in zone 57.8, at about the 366 meter level, by *Sigmodon minor*, but appears once again in zone 58.8, at approximately the 305 meter level, above which it is not recorded. There is no evidence that the two species were sympatric in the Anza-Borrego sequence, but it is likely. The replacement pattern is interpreted as either 1) incorrect stratigraphic assignment of some specimens or 2) the result of competition and possibly habitat modification.

Cotton rats are by far the most commonly recovered small mammals in many deposits of late Pliocene and Pleistocene age throughout the southern United States. Because there are often enough specimens for statistical treatment, and additionally because there is a large body of neontological data from extant species for consultation, cotton rats make ideal subjects for evolutionary and paleoecological study (Martin 1979, 1984, 1986). The occurrence of cotton rats in the Palm Spring Formation of the Anza-Borrego Desert is important, as this is one of the few rock sequences in the United States where cotton rat remains have been recovered in stratigraphically superposed beds that span a considerable amount of time. Consequently, macroevolutionary and macroecological patterns can be documented. This paper represents the results of an initial taxonomic study of the Palm Spring Fm. cotton rat remains, and reports the presence of a new species from the upper, early Pleistocene Vallecito Creek faunal zone. The geology, collecting horizon information, and magnetostratigraphy of the Vallecito-Fish Creek sequence was described by Downs and White (1968) and Opdyke et al. (1977).

The planed and prismatic dentition of cotton rats is more akin in function to that of their northern ecological analogues, the arvicolines, and rather than use the cumbersome cricetine dental terminology of Hershkovitz (1962), we have chosen to use instead the arvicoline terminology of Van der Meulen (1978) for the first lower molar. Homologies are given in Fig. 1. Measurement methods follow Martin (1979) and Czaplewski (1987). Both occlusal and basal lengths are

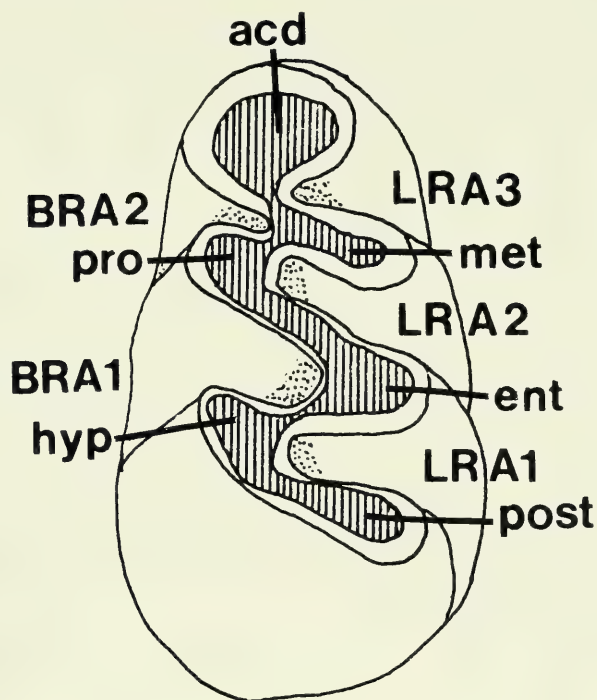


Fig. 1. Topography of a *Sigmodon hispidus* left first lower molar. BRA = buccal reentrant angle, LRA = lingual reentrant angle, acd = anteroconid, pro = protoconid, met = metaconid, hyp = hypoconid, ent = entoconid, post = posterior cingulum or posterolophid. Homologies of reentrant angles to folds, as published by Hershkovitz (1962) and others, are as follows: BRA1 = major fold, BRA2 = first minor fold, LRA1 = second primary fold, LRA2 = first primary fold, LRA3 = first secondary fold.

provided for consistency (see Tomida 1987:103). Abbreviations are as follows: LACM = Los Angeles County Museum, MSU = Michigan State University, L = left, R = right, upper and lower molars (M) indicated by super- and subscript numbers, respectively. The term "zone" as used throughout this paper refers to a specific collecting horizon (level) of Downs and White (1968) in the Vallecito-Fish Creek sediments.

Systematic Paleontology
Order Rodentia Bowdich, 1821
Family Cricetidae Rochebrune, 1883
Sigmodon Say and Ord, 1825
Sigmodon lindsayi, new species

Holotype.—LACM 124161, LM₁, from zone 57.6 (Locality LACM 1114).

Paratypes.—Zone 57.6 (Locality LACM 1114): LACM 124276, LM²; 124136, RM₃; 124117, RM₁; 3402, LM₃; 124154, RM¹; 124144, RM¹; 124122, LM₁; 124146, RM¹; 124139, LM³; 124123, LM₁; 124132, LM₃; 124278, LM²; 124280, LM²; 124260, RM³; 124270, RM²; 124266, LM₂; 124263, RM²; 124261, RM²; 124166, RM₃; 124282, RM₂; 124268, RM²; 124168, RM₂; 124283, LM²; 124169,

LM²; 124272, LM²; 124265, RM²; 124264, RM³; 124129, RM³; 124148, RM₁; 124187, LM²; 124130, RM³; 124190, LM³; 3400, RM₁; 3397, LM₁; 124126, LM₁; 124120, LM₁; 124135, RM³; 124111, RM₁; 124140, LM³; 124188, RM¹; 124138, LM³; 124191, RM₁; 124134, RM³; 124193, LM₃; 124192, LM₃; 124152, LM¹; 124157, LM¹; 124162, RM₃; 124153, LM¹; 124143, RM¹; 124133, RM³; 124124, LM₁; 124155, LM¹; 124131, RM³.

Horizon and type locality.—Collecting zone 57.6 (Locality LACM 1114) of Downs and White (1968), approximately 366–305 meters from top of the Vallecito-Fish Creek sequence, Palm Spring Formation, Anza-Borrego Desert State Park, San Diego Co., California; early Pleistocene (early Irvingtonian land mammal age).

Referred specimens.—The following specimens were also recovered from the Vallecito Creek-Fish Creek sequence of the Palm Spring Formation.

Zone 53.8 (Locality LACM 4963): LACM 122964, RM₁.

Zone 55.5 (Locality LACM 1615): LACM 124242, RM¹; 124238, LM₁; 124251, LM¹-M³; 124257, LM₃; 124258, LM²; 124248, part R mandible with M₁-M₂; 124252, L maxillary fragment with M¹-M²-M³; 124233, RM²; 124249, part L mandible with M₁-M₂-M₃; 124234, LM₂; 124259, LM₃; 124235, RM³; 124236, LM²; 124241, LM¹; 124240, RM₁.

Zone 55.9 (Locality LACM 1297): LACM 6940, part R mandible with M₂-M₃.

Zone 57.7 (Locality LACM 1461): LACM 124197, part R mandible with M₁-M₂-M₃.

Zone 58.8 (Locality LACM 1114): LACM 3396, RM¹; 7037, RM₂; 3399, LM₃; 3401, RM₂.

Diagnosis.—Size large, teeth hypsodont (Table 1, Fig. 2): anteroconid of M₁ wide, anteroposteriorly flattened, symmetrically extended both labially and lingually, and with an occasional enamel atoll in teeth with little wear; metaconid often bulbous and posteriorly directed; protoconid often triangular; lingual reentrant angle (LRA) 2 deep and anteriorly directed; first lower molar with either three or four well-developed roots.

Etymology.—Named in honor of Everett H. Lindsay, whose research on the correlation of upper Pliocene and Pleistocene North American sediments provides a modern framework for evolutionary studies.

Description.—The following description applies to both the holotype and paratype material. Measurements of the dentition are presented in Table 1.

M₁: The anteroconid is large and, in teeth with moderate wear, anteroposteriorly flattened (Fig. 3). It has both labial and lingual extensions. Reentrant angles are narrow and similar to most other cotton rat species except modern *Sigmodon leucotis*, in which the reentrant angles are wide and the M₁ appears long and narrow. In teeth with little or moderate wear, LRA3 and BRA2 directly abut, with only a thin isthmus of dentine connecting the anteroconid and protoconid. This isthmus may widen in heavily worn teeth. Lingual reentrant angle 2 is often deep and anteriorly extended, where it may nearly touch the enamel wall of BRA2. In specimens from Zone 57.6, the metaconid is bulbous and posteriorly directed, and the protoconid may appear triangular in outline. An enamel atoll is present in the anteroconid of two of eight specimens, lying just above the junction of BRA2 and LRA3. The atoll is lost with moderate wear. In one specimen, LACM 124111, the anteroconid is isolated from the protoconid-metaconid complex (Fig.

Table 1. Measurements in mm of *Sigmodon lindsayi* dentition. The mean, number of specimens (parentheses) and observed range (below, parentheses) is provided for each tooth by zone. An asterisk indicates either absence of specimens or lack of observed range for single specimens. Ht = height, L = length, Oocl = occlusal, W = width.

Lower molars										
Zone	Crown Ht	M ₁			M ₂			M ₃		
		Oocl L	Basal L	Oocl W	Oocl L	Basal L	Oocl W	Oocl L	Basal L	Oocl W
58.8	*	*	*	*	1.85 (1)	1.91 (1)	2.05 (2) (2.03-2.07)	1.78 (1)	2.09 (1)	1.94 (1)
57.7	1.22 (1)	*	*	2.00 (1)	*	*	*	2.25 (1)	2.60 (1)	2.04 (1)
57.6	1.22 (8) (0.97-1.43)	2.46 (12) (2.15-2.74)	2.88 (12) (2.42-3.10)	1.83 (11) (1.67-1.97)	1.90 (4) (1.72-2.05)	2.25 (3) (1.91-2.46)	2.16 (4) (2.06-2.31)	1.87 (7) (1.46-2.27)	2.33 (7) (1.94-2.51)	2.01 (6) (1.84-2.2)
55.9	*	*	*	*	1.84 (1)	*	2.03 (1)	*	*	1.92 (1)
55.5	1.21 (2) (1.14-1.28)	2.39 (2) (2.20-2.58)	2.58 (2) (2.44-2.71)	1.79 (4) (1.58-2.07)	1.91 (4) (1.70-2.09)	2.22 (2) (2.09-2.34)	2.04 (4) (1.94-2.17)	1.78 (3) (1.62-1.97)	2.23 (3) (2.13-2.32)	1.95 (3) (1.90-1.99)
53.8	1.11 (1)	2.24 (1)	2.46 (1)	1.67 (1)	*	*	*	*	*	*
Upper molars										
Zone		M ¹			M ²			M ³		
		Oocl L	Basal L	Oocl W	Oocl L	Basal L	Oocl W	Oocl L	Basal L	Oocl W
58.8	*	2.22 (1)	2.37 (1)	2.21 (1)	*	*	*	*	*	*
57.6	2.11 (7) (2.02-2.24)	2.47 (7) (2.29-2.68)	2.13 (9) (2.00-2.34)	2.13 (9) (2.00-2.34)	1.80 (9) (1.62-1.99)	2.06 (9) (1.73-2.55)	2.10 (11) (1.77-2.46)	1.72 (12) (1.54-1.97)	1.90 (12) (1.77-2.31)	1.92 (11) (1.66-2.06)
55.5	2.30 (4) (2.05-2.44)	2.80 (4) (2.48-3.06)	2.15 (3) (1.99-2.34)	2.15 (3) (1.99-2.34)	1.77 (4) (1.64-1.91)	2.00 (2) (1.81-2.19)	1.91 (3) (1.83-2.03)	1.85 (2) (1.80-1.89)	1.84 (1) (1.75-1.97)	1.85 (3) (1.75-1.97)

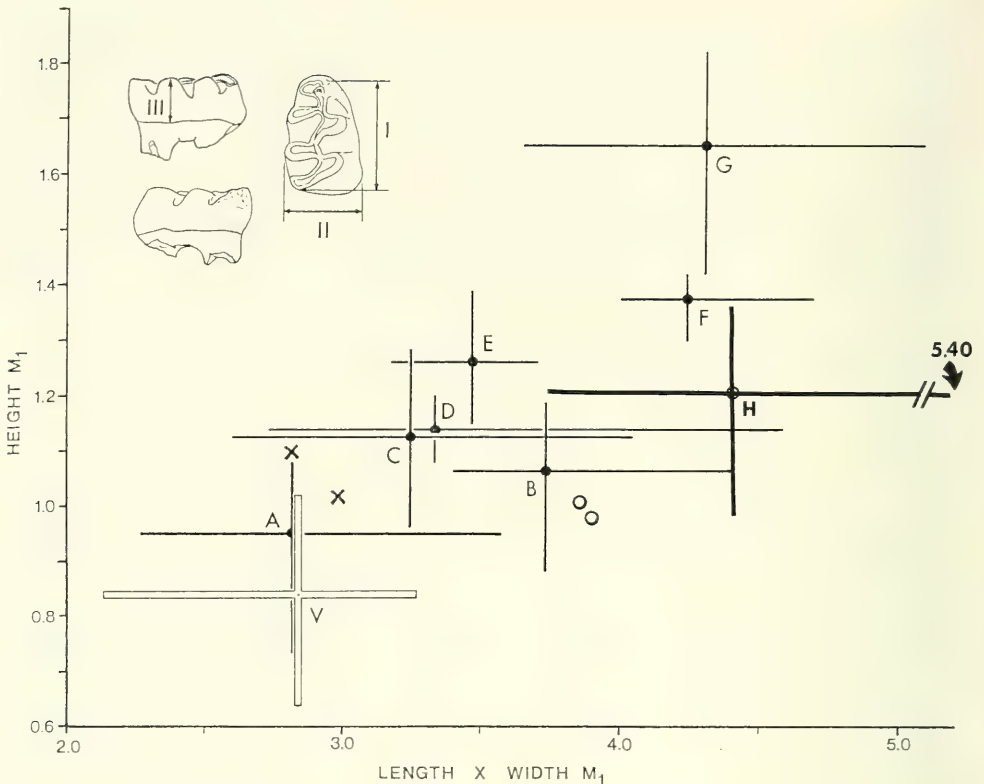


Fig. 2. Crown height (mm) of the first lower molar as a function of occlusal area (mm^2) in *Sigmodon* and *Prosigmodon* species (modified from Martin 1979 and Czaplewski 1987). Inset shows method of taking measurements: I = occlusal length, II = occlusal width, III = crown height at metaconid. V = *S. minor medius* (Verde Formation), A = *S. minor medius*, Rexroad Loc. 3, B = *S. curtisi*, Inglis IA, C = *S. libitinus*, Haile XVIIA, D = *S. bakeri*, Coleman IIA, E = *S. ochrognathus* (extant), F = *S. leucotis* (extant), G = *S. hispidus*, (Reddick IA), H = *S. lindsayi*, Vallecito Creek. Horizontal and vertical lines represent the observed ranges of both measures as they pass through the grand mean. Open circles = *Prosigmodon holocuspis*, x = *P. chihuahuensis*.

3). This is unusual, but it is also occasionally expressed in teeth of extant cotton rat species.

The first lower molar of *S. lindsayi* has either three or four roots. The labial root is well developed, but the lingual root may be absent. Five of eight specimens in which the root pattern could be determined had three roots, the others four.

The single first lower molar from zone 53.8 (LACM 122964) is similar to *S. lindsayi* in size and overall morphology, but two features set this particular specimen apart from those typical for the species. First, the anteroconid, although large and somewhat laterally expanded, is not developed in this regard to the extent as in those from zone 57.6. Secondly, the tooth has only a tiny third (labial) accessory root. This is in contrast to the teeth in zones above 53.8, in which at least three, and occasionally four roots are well developed. It is only provisionally referred to *S. lindsayi*.

Additionally, in one very lightly worn M_1 from zone 55.5 (LACM 124238)

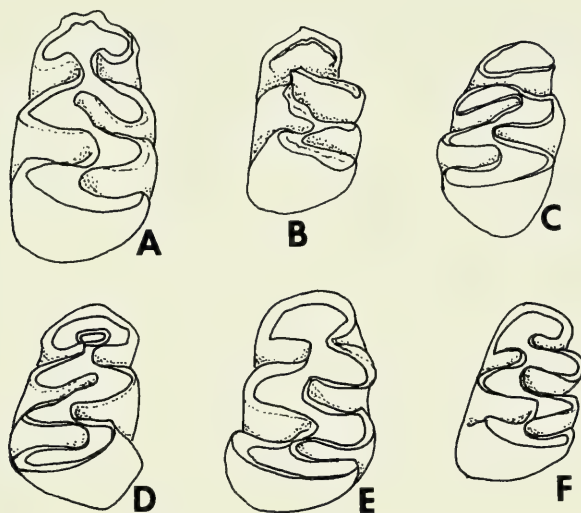


Fig. 3. First lower molars of *Sigmodon lindsayi*, new species, and *S. mascotensis*. *S. lindsayi*: A, LACM 124161, holotype LM₁, $\times 19.2$; B, LACM 124124, unworn, possibly embryonic LM₁, $\times 16.9$; C, LACM 124111, RM₁ with slightly eroded anteroconid—notice separation of metaconid from anteroconid, $\times 17.0$; D, LACM 124117 RM₁, $\times 18.6$; E, LACM 124123 LM₁, heavily worn, $\times 18.6$. *S. mascotensis*: F, MSU 12531, LM₁, from a female, collected 6 mi. W Autlan, 4400 ft, Jalisco, Mexico, $\times 15.0$.

LRA2 is more perpendicular to the midline of the tooth and the tip of the metaconid does not, as a result, appear to extend posteriorly. This may be a function of wear or it could represent a slight morphological change within *S. lindsayi* populations through time.

M₂–M₃: These teeth do not differ in any appreciable way from those of most cotton rats, such as *S. curtisi* and *S. hispidus*. Reentrant folds are relatively deep and narrow, and the anterior cingulum is moderately to well developed on both teeth, as it is in all cotton rats except *S. bakeri* and *S. peruanus* (Martin 1979).

M¹–M²–M³: Likewise, the upper dentition is not diagnostic. These teeth are relatively large (Table 1), but demonstrate no specific characters which would allow separation from other middle Pleistocene species, such as *S. curtisi* or *S. hudspeithensis*.

Comparisons.—*Sigmodon lindsayi* was approximately the size of *S. curtisi* (Martin 1979, 1986). Utilizing Martin's (1984) formula for estimating body mass in cricetine rodents from M₁ length, *S. lindsayi* averaged 76.6 g, with a range of 55.9–116.2 g. Occlusal length was used for these calculations.

The enlarged, symmetrically flattened and laterally extended anteroconid on M₁ is a feature that we have seen only on one specimen of the extant *Sigmodon mascotensis*, the Jalisco cotton rat. The M₁ of MSU 12531, from Jalisco, Mexico, shows a great deal of similarity to the holotype of *S. lindsayi* (Fig. 3). However, the anteroconid is not as greatly extended laterally in two other specimens available for study. A fourth specimen of *S. mascotensis*, with the anterior portion of M₁ broken off, could be added to the analysis for a study of root count. Four well-developed roots are present on all specimens. This is in contrast to the condition in *S. lindsayi*, in which three roots are present in more than half the specimens.

An enamel atoll appears on the anteroconid of other cotton rat species, but is generally rare. We have not, in any case, seen it developed to the same extent in any other species as it was in the two specimens of *S. lindsayi*.

Discussion

Sigmodon lindsayi is an extinct member, along with *S. curtisi*, *S. hudsouthensis* and *S. libitinus*, of the *leucotis* species group of cotton rats (see Martin 1979, 1986 for details of taxonomy), characterized by only three or a combination of three and four roots on the first lower molar. All extant cotton rats in North America except *S. leucotis* have four well-developed roots on M_1 and are members of the *hispidus* species group. Species exclusively with four roots on M_1 are first seen in the fossil record during the late middle Pleistocene. The evidence suggests that the four-rooted M_1 evolved from the three-rooted form.

The teeth of *S. lindsayi* are more high crowned than other extinct members of the *leucotis* species group (Table 1; Fig. 2). Coupled with the high percentage of first lower molars having four roots, it is conceivable that *S. lindsayi* was close to the *hispidus* species grade of dental evolution.

One of the more interesting questions is whether or not the *hispidus* species group evolved from a single common ancestor of the *leucotis* group, or if *hispidus* species group members evolved independently from two or more *leucotis* group species. If the latter, then it may be that *S. lindsayi* is ancestral to *S. mascotensis*.

Specimen LACM 122964, a lower right M_1 from zone 53.8, which we have tentatively referred to *S. lindsayi*, deserves further comment. It is, unfortunately, the only cotton rat specimen recovered from zone 53.8. Zone 53.8 occurs at approximately the 610 meter level in the Vallecito-Fish Creek sequence, well within the Vallecito Creek faunal zone. Zone 55.5, the next overlying interval which contains *S. lindsayi*, is at about the 427 meter level. We do not know how much time occurred during those 183 meters of sedimentation, because there is some doubt about the entire duration of the Vallecito Creek interval (Opdyke et al. 1977). However, if further collecting confirms the dental characters of the cotton rat at zone 53.8, then it may be that this zone represents the transition from a smaller, more generalized species such as *S. minor* to a member of the *leucotis* species group. In size and hypsodonty, LACM 122964 is similar to small specimens of *S. lindsayi* from higher zones. It is for this reason that we provisionally refer the specimen to the latter species. However, accessory roots are minimally developed on M_1 , as in *S. minor*, and the anteroconid of M_1 is also not as exaggerated as it is in typical *S. lindsayi* first lower molars.

We will present a detailed analysis of morphometric change in cotton rat dentitions from the Anza-Borrego sequence elsewhere, but it is interesting to note that *Sigmodon minor*, which is ubiquitous through more than 3048 meters of sediment representing 2.0 million years prior to the first appearance of *S. lindsayi*, is not simply replaced by the latter species during the time represented by the Vallecito Creek sediments. *Sigmodon lindsayi* appears at zone 55.5 (or 53.8), and persists through zone 57.7, but it then is absent from zone 57.8, at which level only *S. minor* is encountered (14 isolated teeth and one mandibular fragment with M_1 - M_3). At the next highest level, zone 58.8, *S. lindsayi* occurs once again, without *S. minor*.

Although we have no inherent reason to doubt the stratigraphic data associated

with the specimens that we have studied, the pattern above has not been recorded from other depositional basins in North America, and we are suspicious that the *S. minor* specimens at zone 57.8 may belong to a lower unit. However, if this is not the case, then the pattern can be explained easily by a combination of competition and climatic modification. Martin (1986) summarized the research on competition among living cotton rats and their arvicolid analogues, and noted that one species of cotton rat rarely tolerates the presence of another *Sigmodon* or *Microtus* species, especially if it is small. Those small cotton rats that have evolved are now extinct, including *S. minor*. Therefore, it seems likely that as populations of *S. lindsayi* became established in the Anza-Borrego area, those of *S. minor* diminished. Zone 57.8 could represent a limited area in which *S. lindsayi* became locally extinct due to an unknown climatic event, allowing *S. minor* to return temporarily. At the periphery of their ranges in Kansas, an interplay of this sort occurs between *Sigmodon hispidus* and *Microtus ochrogaster* (Martin 1986). When winters are cold, populations of *S. hispidus* die off, allowing *M. ochrogaster* to repopulate the area. However, because *S. hispidus* is the more dominant species, wherever they are sympatric, *S. hispidus* generally replaces *M. ochrogaster*.

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Research Note

Collective Vigilance Enhances Feeding Rates of The Opaleye *Girella Nigricans* (Girellidae)

The benefits of schooling for both predator and prey fish have been well documented. Fish in schools are preyed upon less frequently than solitary individuals, and schools of predatory fish feed more efficiently (Neill and Cullen 1974; Bertram 1978; Major 1978; Pitcher 1986). The benefits of collective vigilance in schooling fish have been that their members are able to feed, clean, and conduct other behaviors in relative safety (Pitcher 1986). Collective vigilance in birds has been studied extensively (Vine 1971; Powell 1974; Siegfried and Underhill 1975; Lazarus 1979). These studies indicate that individuals in groups are preyed upon less frequently than solitary individuals. These findings are similar to those of analogous fish studies (e.g., Neill and Cullen 1974; Major 1978). Additionally, Sullivan (1984) found that Downy woodpeckers feed at higher rates in flocks than while solitary. It follows that schooling prey fish would also benefit from the survival value of collective vigilance to enhance feeding rates.

Girella nigricans, a facultative schooling fish (as defined by Breder 1967 and Shaw 1970), was studied in the field to determine if collective vigilance of aggregated conspecifics enhanced the feeding rates of facultative schools when compared to solitary fish. *G. nigricans* is an abundant herbivorous fish (Mitchell 1953) found in the intertidal zone and kelp beds from Baja California to San Francisco (Miller and Lea 1972). *G. nigricans* is a natural prey item for such predators as the sea lion, *Callorhinus ursinus* (Smith et al. 1980, 1981) and the cormorant, *Phalacrocorax pelagicus* (Ainley et al. 1981 and personal observation).

To test the hypothesis of enhanced feeding rates, I observed individual *Girella nigricans* in groups of various compositions: solitary, small groups (2-6 members), and facultative schools (more than 6 members). *G. nigricans* of 6 to 9 cm total length (TL) were observed because they consistently maintained a smaller home range than the larger conspecifics (pers. obs.). The observations were made while snorkeling at depths of 1 to 3 m at the rock jetty in Big Fisherman's Cove, Santa Catalina Island. Data were collected in the morning and afternoon during two weeks in November 1985, and one week in May 1986. A solitary individual *G. nigricans* or an individual within a facultative school was chosen for observation, approached slowly, with a minimum of surface disturbance, and followed. Feeding rates were measured in bites per minute (bpm) and collected during 3 to 5 minute periods. Data were recorded at pre-measured distances of 1.0, 1.5 and 3.0 m to determine diver-induced feeding interference. I speculated that a diver in a dark wet suit would imitate the appearance of a predator which could inhibit the feeding rates of the fish.

To confirm dietary composition and food abundance, foregut analysis was performed on 15 *G. nigricans*. Foregut contents were preserved in a 10% formalin solution within one hour of capture, and analyzed under Baush and Lomb dis-

Table 1. Feeding rates of solitary *Girella nigricans* at different distances from a diver. DISTANCE = the distance from observer to *G. nigricans*, AVG. BPM = the average bites per minute for an individual, S.D. = standard deviation, N = number of observations.

DISTANCE (m)	AVG. BPM	S.D.	N
1.0	12.60	5.25	9
1.5	17.10	3.37	9
3.0	21.10	6.09	9

secting microscopes. Algae were identified with the use of Abbot and Hollenberg (1982).

Correlation analysis was employed to analyze feeding rates of aggregated *G. nigricans*. Two way analysis of variance without replication, was used for determining diver-induced effects on feeding rates of solitary individuals and facultative schools at specific distances. Additionally, unpaired t-tests were employed to compare feeding rates of solitary and aggregated fish.

Solitary *Girella nigricans* were wary, easily alarmed, and difficult to observe. Some were quick to join small groups or nearby facultative schools. Solitary *G. nigricans* fed at the fastest rate (21.1 bpm) when diver distance was 3.0 m (Table 1). As observation distance decreased, the feeding rate decreased significantly (two way analysis of variance, $P < 0.05$., Table 2). Solitary fish would flee or hide among the rocks when approached to 1.0 m. Therefore, subsequent data were collected at 3.0 m.

Small groups (2–6 members) of *G. nigricans* formed when one or two individuals separated from a facultative school, frequently attracting one or two others. Group size varied constantly. Small groups were usually joined by a facultative school, another small group, or an individual. The small groups would remain distant from the original school for one to two minutes. Accurate data could not be recorded because group size was never consistent for the length of time required to adequately collect data.

Facultative schools of *G. nigricans* (7 to 37 members) were less wary than solitary individuals or small groups and could be approached to approximately 0.6 m before diver-induced interference disrupted feeding behavior. All subsequent data were collected at 3.0 m, to be consistent with solitary data. There were no significant difference between feeding rates of individuals within facultative schools at varying distances; i.e., two way analysis of variance, 1.0 m, 1.5 m, and 3.0 m, $P > 0.05$.

Individual members of facultative schools fed at significantly higher rates than

Table 2. Two way analysis of variance, without replication, for solitary *Girella nigricans*. Distances were 1.0, 1.5 and 3.0 m. F-tests were calculated at the 0.05 level.

Source	df	SS	MS	F	P
Fish	8	265.0	33.1	1.46	>0.05
Distances	2	321.2	160.6	7.11	<0.05
Error	16	360.8	22.6		
Total	26	947.0			

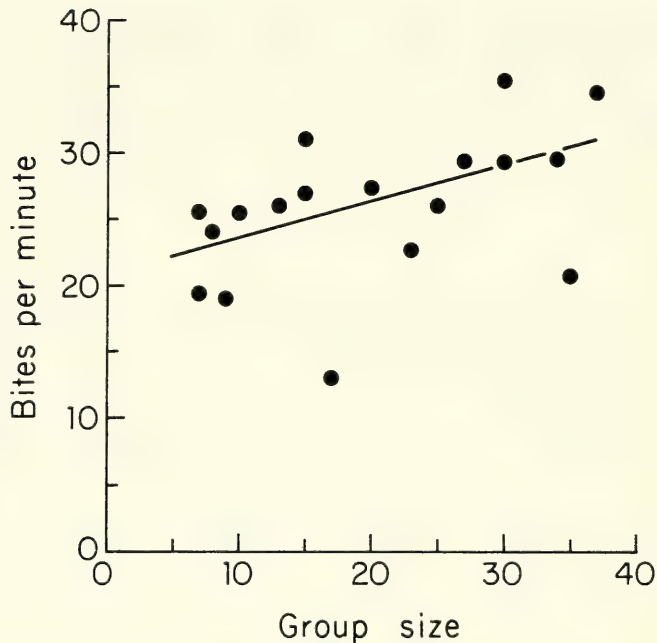


Fig. 1. Group size or numbers of individual *Girella nigricans* per group and bites per minute. Each dot represents an average bites per minute for individual within the group.

solitary individuals (t-test, $P < 0.05$, $N = 30$, Table 3). As facultative schools increased in size, the average bpm for individuals within the school increased (Fig. 1). Group size significantly affected individual feeding rates within the school ($r = 0.475$, $P < 0.05$, $N = 18$, Fig. 1).

The analysis of foregut contents determined that the food source for *G. nigricans* was readily abundant during the study. The diet of *G. nigricans* consisted of algae within the following genera: *Ralphsia*, *Pseudolithoderma*, *Giffordia*, *Gelidium*, *Enteromorpha*, and *Ulothrix*. Due to the semi-digested nature of the algae, identification to species was impossible. These algae were consistent with the seasons and location of the study.

The data in this study clearly demonstrated that feeding rates increased significantly as group size increased in facultative schools of *Girella nigricans*. Additionally, the feeding rates of solitary *G. nigricans* were significantly lower than those within facultative schools (Table 3). These results imply that the collective vigilance of facultative schools of *G. nigricans* allowed individual members to spend more time feeding as compared to solitary fish. These findings are consistent with those of Pitcher (1986), who found that members of a group reduced their vigilance level and allocated more time to feeding, and Sullivan (1984), who found Downy woodpeckers fed at higher rates in flocks. In addition, Godin et al. (1988) found that, in the laboratory, individual vigilance decreased as group size increased. Previous studies performed to determine the benefits of schooling in fish focused on: The preventing of territoriality (Robertson et al. 1976); the deflection of predation (Neill and Cullen 1974; Bertram 1978; Major 1978; Pitcher 1986); and collective vigilance (Godin et al. 1988). The study of enhanced feeding rates

Table 3. Feeding rates for *Girella nigricans*, observed at a distance of 3 m. FISH # = the fish number, #/GROUP = the number of fish in a group, either 1 or more, AVG. BPM = average bites per minute, S.D. = the standard deviation, N = the number of observations per fish.

#/GROUP	AVG. BPM	S.D.	N
Solitary			
1	11.30	2.75	4
1	11.50	1.00	4
1	9.30	5.50	3
1	16.80	3.59	4
1	13.30	4.57	4
1	8.00	1.73	3
1	23.80	4.21	5
1	12.70	6.25	6
1	13.70	1.89	7
1	15.80	3.49	5
1	17.20	4.87	5
1	11.50	5.97	4
Grouped			
27	29.30		3
20	27.30	6.65	3
15	31.00	6.02	2
25	26.00	2.83	1
30	35.50	—	4
7	25.50	4.79	4
37	34.60	1.29	5
17	13.00	9.02	2
8	24.00	6.00	3
9	19.00	6.70	2
34	29.50	3.87	2
15	27.00	7.65	2
35	20.80	2.50	4
30	29.20	4.29	9
10	25.40	2.72	8
23	22.60	4.88	5
13	26.00	—	1
7	19.20	1.79	5

as an additional benefit of schooling in prey fish is a relatively new concept; paralleled, however, by those studies performed on birds (Vine 1971; Sullivan 1984) which draw similar conclusions of enhanced feeding rates as a direct benefit of collective vigilance. Therefore, the results of those studies support the hypothesis and results of this study indicating that the collective vigilance of a facultative school of *G. nigricans* significantly enhanced the feeding rates of individuals within the school.

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COVER: *Hippothoa hyalina*, a cheilostome bryozoan which encrusts gastropod shells of *Tegula funebris* inhabited by the hermit crab *Pagurus samuelis*. Colony shows large females with perforate brood chambers (ovicells), autozooids with apertures having a U-shaped proximal sinus, and miniature male zooecia.